

ECOLOGICAL EFFECTS OF GRAZING AND TRAMPLING ON MOUNTAIN VEGETATION IN NORTHERN SWEDEN



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The dissertation is based on the following three papers:

I. Emanuelsson, U. 1984. Dynamics of dwarf shrub heaths in relation to grazing of small rodents in the Torneträsk area, northern Sweden.

II. Emanuelsson, U. 1984. Short-term effects of trampling in subalpine and alpine ecosystems in the Torneträsk area, northern Sweden.

III. Emanuelsson, U. 1984. Vegetation zonation on tracks through dwarf shrub heaths in the Torneträsk area, northern Sweden.

Reference to these papers is made by using the respective Roman numerals.

In nature, mechanical impact of different types such as trampling and grazing of animals is important for the dynamics of the vegetation.

Man may also be a principal vector for mechanical impact, for example, by trampling. Concern for the probable damage to vegetation caused by an increasing number of tourists in the Torneträsk area led to the work presented here, being initiated in 1977. The effects of both natural mechanical impact (I) and those of human trampling were studied (II, III).

The investigations were carried out in the Torneträsk area (II) in the northwesternmost part of Sweden ($68^{\circ} 20' - 30' N$ and $18^{\circ} 10' - 20' E$ Gr). The area is characterized by strong climatic gradients and widely varied vegetation.

The vegetation in the area covers a gradient from subalpine birch forest (Betula pubescens ssp tortuosa with Scots pine (Pinus silvestris) in some places, to high alpine tundra.

The human influence on the vegetation in the area is regarded as small compared to most other areas in Sweden. Pronounced touristic influence on the vegetation is regarded as a recent phenomenon.

A number of animals certainly cause a considerable mechanical impact upon the vegetation in the area, e.g. reindeer, moose, autumnal moths and small rodents, the small rodents perhaps being the most important animal group in this respect. This form of impact must therefore be considered as well, in order to evaluate the magnitude of the human influence on the vegetation caused by trampling. Is the human trampling only marginal compared to the "natural" mechanical impact or will it affect the ecosystem in such an extensive way that it cannot be confused with, e.g., the impact of small rodents?

The effects of grazing by small rodents, mainly Clethrionomys rufocanus, upon Empetrum hermaphroditum-dominated dwarf-shrub heaths were studied (I). Much of the grazing in peak years seemed to take place under the snow in winter. Crust formation in the snow 5-10 cm above the soil surface causes the rodents to graze only the lower parts of the plants, leaving the upper parts frozen into the snow. More dwarf-shrubs were therefore killed than consumed.

There was a marked difference in the amount of killing of the dwarf-shrub vegetation during the winter 1977/78 along a oceanic-continental climatical gradient studied. Approximately 80% of the aboveground phytomass in the oceanic parts was grazed, whereas only approximately 10% in the continental parts. Probably the oceanic climate was a positive factor for the formation of crust horizons in the snow leading to a larger non-consumptional killing.

On hilltops in sub-alpine birch forest the winter-grazing was very low, on hillsides it was high and, finally, it was low at the bottom of the hills, probably as a result of different snow depths and crust formations.

In the years following the killing of the vegetation the rodents in the dwarf-shrub heaths caused a rise in the abundance of the grasses, in the first instance, followed by Vaccinium myrtillus and later by Vaccinium vitis-idaea. It can be assumed that the dominating Empetrum hermaphroditum is made less dominant periodically in many dwarf-shrub heaths due to winter-grazing by small rodents and thereby favouring grasses and Vaccinium species.

It was also found that rodent grazing of Vaccinium vitis-idaea made the grazed parts of the plants less palatable for later grazing by small rodents.

Two types of trampling impact were studied; the short-term effects on vegetation not earlier trampled (II), and the long-term effects on tracks, leading to zonation of plants with different resistances (III).

The short-term effects were studied in a number of sub-alpine and alpine vegetation types using an experimental plot formed like a fan or a circle sector (II). In this, a trampling gradient was produced by walking a number of times from the tip of the sector to the arc of the circle and successively reaching different positions on the arc. The reaction of the different vegetation types was measured after a few months, and after one and two years after the trampling had taken place. Cover, species number, standing crop and diversity were measured.

The ranking scale of the measured vegetation types in respect of vulnerability to trampling was approximately the same no matter what parameter was used. Fen vegetation was the most sensitive type, withstanding only about 30 passages if its cover two months after trampling was not to fall below 50% of its original value. Thereafter came dwarf-shrub heaths with about 60 passages, and mires with dwarf-shrubs with about 70 passages. Meadow vegetation types could withstand much more trampling, in some cases several hundred passages. Also the meadow vegetation types recovered totally the fastest, in some cases in two years after 1600 passages. Comparing relatively similar vegetation from high altitudes (1200m) with that of low altitudes (350-600 m) it was evident that high altitude vegetation types were not more sensitive than the others, but they recovered more slowly.

Trampling early or late in the season seemed to affect especially meadow vegetation types less than trampling in the middle of the season. Also, distributing the trampling on 3-5 occasions had a larger effect than trampling concentrated to only one occasion or spread out on 65 occasions.

Long-term effects were studied on tracks passing through Empetrum hermaphroditum-dominated dwarf-shrub heaths (III). On three tracks four transects on each were placed out randomly. Here the zonation of plants was studied as well as the subsequent succession after ceased trampling. Also, twelve old abandoned tracks were studied to document the later stages in the succession taking place in abandoned tracks through Empetrum-dominated vegetation.

In tracks used (around 2000 passages) on flat ground without obstacles a narrow vegetation-free zone in the middle of the track is evident, which is bordered by a zone dominated by small cryptogams, in turn being bordered by a zone with cryptogams and grasses (Festuca ovina, Deschampsia flexuosa or Calamagrostis lapponica). Approximately 2-3 dm from the middle of the track Vaccinium vitis-idaea and V.myrtillus are dominant, but outside this zone Empetrum hermaphroditum and V.uliginosum successively appear.

When trampling ceases grasses will invade the center of the track in about one year, very soon followed by Vaccinium myrtillus and V.vitis-idaea. Empetrum hermaphroditum is much slower to recover, probably as a result of its lack of rhizomes. It seems that narrow tracks need some decades to recover totally, but it is also clear that wider tracks need much longer periods for regeneration.

Comparing the effects of the mechanical impact of rodents on the vegetation with those of the human trampling impact it is evident that there are both similarities and differences.

It is striking that many species are negatively influenced by rodent mechanical impact and trampling in a similar way. One obvious example is Empetrum hermaphroditum. It is also evident that there are great similarities in the successions taking place on abandoned tracks (III) or trampled circle sectors (II) on one hand, and in areas heavily grazed in winter by rodents (I) on the other.

The rate of recovery of the vegetation varies considerably depending on the type of impact. Tracks are slowest to disappear, especially if they have been trampled for a long time and are wide (III). Experimentally trampled areas like the circle sectors recovered faster (II), but rodent-grazed areas

were the fastest to recover (I).

The compacting of the soil in the trampled areas was probably a negative factor with respect to recovery, compared to the rodent grazed areas which were not at all compacted.

Also the fact that there does not seem to be any living rhizomes in the soil in old tracks (III) or very extensively trampled experimental plots must have prevented a fast recovery in those areas.

In summary: In some years the mechanical impact by small rodents has a considerable effect on the dwarf-shrub heaths over large areas and this impact, in the short run, is much larger than the impact caused by human trampling.

The effects of human trampling, especially in the dwarf-shrub heaths, remain for long periods, in contrast to the grazing effects of rodents. However, it is not possible to judge the impact of grazing of small rodents without careful observations of permanent investigation plots.

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I. DYNAMICS OF DWARF SHRUB HEATHS IN RELATION TO GRAZING OF
SMALL RODENTS IN THE TORNETRÄSK AREA, NORTHERN SWEDEN

DYNAMICS OF DWARF SHRUB HEATHS IN RELATION TO GRAZING OF SMALL RODENTS IN THE TORNETRÄSK AREA, NORTHERN SWEDEN.

ABSTRACT

The effects of grazing by small rodents mainly Clethrionomys rufocanus upon Empetrum hermaphroditum-dominated dwarfshrub heaths were studied during 1977-1981 in the Torneträsk area in northern Lapland, Sweden. Much of the grazing in peak years seemed to take place in winter under the snow. Crust formation of snow 5-10 cm above the soil surface made only the lower parts of the plants available to the rodents, leaving the upper parts of the plants frozen into the snow. A lot more dwarf-shrubs were therefore killed than consumed.

There was a marked difference in the amount of the dwarf shrub vegetation killed during the winter 1977/78 along a oceanic-continental climatical gradient studied. Approximately 80% of the aboveground phytomass was grazed in the oceanic parts of the gradient but only approximately 10% in the continental parts. Probably the oceanic climate was a positive factor for the formation of crust horizons in the snow leading to a larger non-consumptional killing of the dwarf shrubs in oceanic areas.

On hilltops in sub-alpine birch forest the winter-grazing was low, on hillsides it was high and, finally, at the bottom of the hills it was low, probably as a result of different snow depths and crust formations.

In the following years, killing of the vegetation by rodents in the dwarf shrub heaths caused a rise in the abundance of the grasses in the first instance, followed by Vaccinium myrtillus and later by Vaccinium vitis-idaea. It can be assumed that the dominating Empetrum hermaphroditum is made less dominant periodically in many dwarf shrub heaths due to winter-grazing by small rodents, thereby favouring grasses and Vaccinium species.

It was found that rodent grazing of Vaccinium vitis-idaea made the grazed part of the plants less palatable for later grazing by small rodents.

1 INTRODUCTION

1.1 Herbivory in northern vegetation.

Small rodents are known to have a substantial impact on ecosystems in arctic (Schultz, 1964, 1969), in subarctic (Kalela, 1957, Kalela et al., 1971) and in boreal areas (Golley et al., 1975). The literature dealing with such influence has recently been reviewed by Ericson (1977) studying a 4-year population cycle of small rodents. Earlier, Tast (1974) carried out a similar study. Both emphasize the importance for the further vegetational development of which structural parts of the plants that are grazed. The former author also stresses additional rodent effects such as fertilizing and destruction of the moss layer. Oksanen (1981) demonstrated the importance of voles grazing on some dwarf shrub species. Haukioja et al. (1983), among others, discussed the causes of their annual and seasonal cycles.

Larsson (1978) states that at Abisko in the Torneträsk area Clethrionomys rufocanus and, to a lesser extent, Microtus agrestis, are the rodents most likely to occur in the Empetrum-dominated vegetation.

There are also other types of herbivory in subarctic vegetation.

The impact of caterpillars has been described by Tenow (1975), mainly studying the influence of Epirrata autumnata (earlier named Oporinia autumnata) and Operophtera brumata on the tree layer. Sandberg (1958) mentions that the herb layer may also be affected by these insects, although results of detailed investigations are lacking. Domestic reindeer grazing may have considerable effects on the vegetation as shown, e.g., by Helle & Aspi (1983).

In 1977, the present author started an investigation on the effects of mechanical impact, mainly caused by human trampling, for the structure and dynamics of mainly subarctic heaths dominated by Empetrum hermaphroditum in the Torneträsk area (68°00' N; 18°00' - 20 00' E), (Fig.1). Besides human influence, some of the mechanical impact caused by animals



grazing on the vegetation was studied.

In this paper the influence on the vegetation dynamics, mainly caused by grazing of small rodents will be discussed. Later papers (Emanuelsson, 1984a and b) will mainly consider the effects of human trampling.

1.2 Winter grazing

Observations in the Torneträsk area by the present author indicate that grazing by small rodents during the winter may be of great importance.

Grazing is possible because of the development of a space between the snow layer and the ground, i.e. the sub-nival space (Coulianos & Edström 1971). In February, 1981, and April, 1982, the snow was excavated in some sites in the Torneträsk area and the Njoutjousvagge area of central Lapland by the author. On these occasions it was observed that the tops of the dwarf shrubs were frozen into the snow while the lower parts were exposed in the sub-nival cavity and then accessible to small rodents. Only the top shoots of Vaccinium myrtillus could be pulled to some extent out of the snow, whereas this was not possible for the other species (mainly Vaccinium vitis-idaea and Empetrum hermaphroditum) since their winter-green leaves kept them effectively frozen into the crust.

From these observations (made mainly in Njoutjousvagge) three types of access, and thus grazing, were apparent: (1) The snow could be densely packed, thereby preventing access by the rodents. (2) The snow could be more loosely packed, allowing the rodents to graze in tracks through the lower layers of the snow. (3) The snow could be very loosely packed, allowing grazing to occur over large areas beneath the snow. In the latter case, if an ice layer existed 2-7 cm above the ground surface, the tops of dwarf shrubs detached by grazing from below, remained in the snow. However, if the ice layer was absent, no tops of the dwarf shrubs remained (Fig. 2).

From these observations it was also inferred that the species were affected differently. Empetrum hermaphroditum lost its top shoots, where most of their apical meristem is situated. Thus the grazing of Empetrum must hamper its growth because living parts of the plant below the ground surface regenerate very rarely. Recolonization must take place by branches "invading" from outside the grazed area (Emanuelsson, in prep.). It was frequently observed in the investigation area that Vaccinium vitis-idaea also lost its shoots. However, it regenerates quite easily from buds on below-ground rhizomes (Teär 1972). This also applies to V. myrtillus, although the grazed aerial shoots also often showed subsequent proliferation (Emanuelsson, in prep.). Only insignificant regeneration from the rhizomes of V. uliginosum has been observed in the Torneträsk area. Recolonization occurs mainly by the invasion of branches from outside the grazed area. Recolonization occurs mainly by the invasion of branches from outside the grazed area (Emanuelsson, in prep.). According to Warming (1908), regeneration from rhizomes is common, however. Calamagrostis lapponica has an extensive rhizome system from which new shoots were found to develop after grazing. In contrast, Festuca ovina and Deschampsia flexuosa, being tufted grasses, regenerated from seedlings in the study plots after grazing (Emanuelsson, in prep.).

However, even if these observations suggested that winter grazing by small rodents is quite substantial in the vegetation studied, - at least some years, and possibly also more influential to the plants than grazing during the summer-, it is of course impossible to relate all signs of herbivory obtained and discussed in this paper to winter grazing alone.

2. INVESTIGATED VEGETATION, SITES AND METHODS

2.1 Empetrum heaths

Empetrum nigrum or E. hermaphroditum can be found on many types of poor soils around the whole of the northern hemisphere (Hultén, 1950). In many subarctic, arctic, sub-alpine and

alpine environments, E. hermaphroditum may be the dominant vascular plant, often in association with other dwarf shrubs. Dwarf shrub heaths dominated by E. hermaphroditum are found in areas on both sides of the tree-line in Scandinavia. Maps of the vegetation of the Swedish mountain chain (Vegetations-kartor 1979-84) published by the Swedish Environmental Protection Board show that a zonation of heaths occurs in the mountains. Grass-dominated heaths occur at the highest altitudes above drier Empetrum types while wet heaths occur at even lower altitudes. Below the tree-line the variation of the types is greater than above it, Vaccinium myrtillus being common and often co-dominant together with Empetrum here. Flat areas in the north-eastern part of the Swedish mountain chain are dominated by lichens but Empetrum is still an important component of the vegetation (Vegetationskartor 1979-84).

2.2 Sites and experiments (see Table 2 for a summary).

All investigations were carried out in heath vegetation of the "Empetrum type" and "Empetrum-Vaccinium myrtillus type" as described by Sonesson & Lundberg (1974) near Abisko in the Torneträsk area (Fig.1 and Table 1.).

The western part of the area lies within the Scandinavian mountain chain, the altitudinal range being 341 - 1,991 m above sea level. Approximately 40% of this area is alpine tundra whereas 60% is below the tree-line. The forests are dominated by the mountain birch, Betula pubescens ssp. tortuosa. For further information on the investigation area, see Sonesson & Lundberg (1974).

Nomenclature for cryptogams is according to Krok & Almquist (1962), for vascular plants to Lid (1974) and for mammals to van den Brink (1958).

2.2.1 Permanent investigation plots

One series of investigation plots (Table 2,A.) , originally established for trampling studies, was placed near the Abisko Scientific Research Station. The tree canopy covered 15-20% . Eight main plots, each consisting of 16 sub-plots (2.5 dm^2), were randomly placed all over the area. In early June and in late August in each of the years from 1977 to 1980 the cover of the species of these plots was recorded.

A detailed study of the vegetation dynamics following grazing was carried out in an area of $25 \times 40 \text{ m}$ within which 15 plots were randomly placed (Table 2,B). Each plot was $0.5 \times 0.5 \text{ m}$ and was divided into 400 $2.5 \times 2.5 \text{ cm}$ sub-plots. The 15 plots were only selected if more than 50% of their area was estimated to have been affected by grazing in the winter 1977/78. In these 15 plots the presence or absence in the 400 sub-plots of Empetrum hermaphroditum, Vaccinium myrtillus, V. vitis-idaea and grasses was noted. The presence of living shoots in 1977 was estimated from the remaining parts of the shoot recorded in 1978. Investigations were also undertaken in 1979, 1980 and 1982. In addition to these 15 plots, a similar plot which was dominated by Empetrum and heavily grazed was also observed, together with 4 plots for investigations of V. vitis-idaea and 3 for V. myrtillus. The latter plots were located in the immediate vicinity of the 15 investigation plots and were used for studies of biomass changes due to grazing (Table 2,E).

Finally 500 m^2 squares were placed in three sites (b,i,m), (Tab 2,H) to investigate the proportion between the above-mentioned species and the grasses as well as the amount of grazed parts (Tab 5.)

2.2.2 Sites showing regional pattern of grazing

Nine sites ($25 \times 40 \text{ m}$ in size), (Fig. 3), (Table 2,C) were chosen in Empetrum-dominated vegetation, where Empetrum hermaphroditum covered 40 to 60 % of the surface. Within each

site the altitudinal difference was maximally 2 m, apart from sites i and m which had a greater altitudinal difference and where Betula nana was more abundant. The areas were located below an altitude of 700 m above sea level.

In sites e, j and k the grazing was estimated roughly in the same way as described above but more extensively.

In the other sites, series of 1 dm broad transects were established. At each site there were 17 transects each of 25 m. and divided into 250 1 dm^2 sub-samples. Each area consisted, therefore, of 4,250 1 dm^2 sub-plots.

Within those sub-plots the presence or absence of grazed plants was noted, grazing being defined as more than 50% of the shoots touched as evidenced by dead tissues or cut stems.

In addition to those sites more extensive qualitative observations of grazing in Empetrum-dominated places were also carried out, especially above 750 m in altitude.

2.2.3 Sites showing local patterns of grazing.

Ten profiles similar to those described above were established over an area measuring 42 ha, 500-800 m SSW Abisko Scientific Research Station, to show the influence of grazing along slopes. Three of these were randomly selected and studied in detail (Fig. 4 a-c), (Table 2, D).

2.2.4 Estimation of the grazed phytomass

Fifteen 2.5 dm^2 plots were established randomly in areas where more than 50% of the vegetation had been grazed, i.e. the same criteria were used as those for selecting the plots described under 2.2.2 above.

In each plot, the detached phytomass was collected and weighed. Older, dead leaves of Vaccinium myrtillus were also collected and counted in an attempt to estimate the phytomass

of this species before the winter grazing. This was estimated from the relationship that 1 leaf is supported by 0.07 g of stem, a factor suggested by Flower-Ellis (1971). The phytomass of the other species was estimated by counting the number of stems, which remained on the ground surface. Empetrum and Vaccinium vitis-idaea were then collected from parallel plots which had not been grazed but contained approximately the same density of shoots. These data are presented together with estimates of phytomass detached but not consumed (Table 2,E).

2.2.5 Grazing pressure

No data on the population density of small rodents in the area are available for the period of this investigation in the investigation area. However in an attempt, to estimate the grazing pressure the quantity of rodent faeces deposited in the vegetation was measured (Table 2,F). Faeces were collected and counted from all the plots described above (Table 6). Only fresh faeces, i.e., black and plastic droppings, were counted.

2.2.6 Grazing experiments

A tentative experiment on caged animals was carried out during the summer of 1978 (Table 2,G). The experiment was conducted on Clethrionomys rufocanus as this is the most common species in the investigated vegetation (Larsson 1978). Five animals were given various combinations of food on five occasions. The combinations of food were randomly selected for each animal on each occasion but as the experiment progressed, each individual had the opportunity to eat different combinations of food. Eleven species of plants were tested in combinations of 2, 3 or 4 species. The preference could then be determined within the group Empetrum hermaphroditum, Vaccinium myrtillus, V. vitis-idaea and V. uliginosum. Similarly, the grazing preference was determined among the grasses Calamagrostis lapponica, Festuca ovina and Deschampsia flexuosa and among the mosses Polytrichum commune, Pleuro-

zium schreberi, Hylocomium splendens and Sphagnum species. The preferred species from within each of the 3 groups were then compared with each other and, finally, Linnaea borealis was compared with Empetrum hermaphroditum and V. vitis-idaea. (Table 7).

2.2.7 Studies on grazed rhizome systems

Twelve Vaccinium vitis-idaea rhizome systems were studied in 1978 and 1982. The grazing of areal shoot systems in common rhizome systems was the objective of the study. As it is extremely hard to tell whether a shoot system belongs to the same rhizome system as another shoot system without digging up the plants, many more shoot systems were registered in 1978 than were finally used for the study. In 1982 the plants were dug up and the actual relationships between the shoot systems could be revealed.

3 RESULTS

3.1 Regional differences in grazing

The effect of grazing by rodents during 1977-78 varied considerably on a regional scale in the Torneträsk area. Areas with an extensive grazing had a patchy distribution.

There were no differences in grazing between plots above and below the tree-line. Although only based upon few observations from areas higher than 750 m above sea level, there seems to be much less grazing here than in vegetation below 750 m above sea level.

A geographical "grazing gradient" was evident. The grazing seemed to have been most intensive in the NW part of the Torneträsk area, and least in the SE part (Fig. 3).

3.2 Local differences in grazing

There was also a patchy distribution of grazing on a local level. No correlations were found between grazing and factors such as canopy cover and soil moisture. The upper and lower parts of the slopes on smaller hills in the mountain-birch forest (Fig. 4a-c; 2a-c) were grazed less than the middle parts of the slopes. This phenomenon, however, was not evident on slopes on hills situated more than 100 m above the tree-line. Below the tree-line small hill tops were touched less as well as small depressions, i.e. grazing varied according to the microtopography (Fig. 4a-c).

When looking at the detailed grazing choice in the field by the rodents there seemed to be just one significant correlation (the combination Vaccinium vitis-idaea - Empetrum hermaphroditum) between the amount of grazing that had happened to any of the species: Empetrum hermaphroditum, Vaccinium myrtillus, V. vitis-idaea or the grass species (Table 4).

The rodents seemed also to graze a higher proportion of Vaccinium myrtillus when this species was common. The other species were not proportionally more grazed when they occurred more abundantly, however (Tables 5, 6).

Detailed studies of the distribution patterns of the various species showed long-term trends in relation to grazing. In some cases, Empetrum hermaphroditum had totally disappeared from some areas and recolonization seemed to occur from a few neighbouring ungrazed plots by the development of branches from several initials on the untouched shoots, as illustrated in Fig. 7.

Empetrum shoot systems that had been recently grazed, were grazed again four years later (Fig. 7). On the other hand, in most cases shoots of Vaccinium vitis-idaea were not touched if they belonged to a rhizome system that had been recently grazed. Out of 12 rhizome systems (see 2.2.7) there were none in which grazing had taken place upon the same shoot system or on neighbouring shoot systems both in 1978 and 1982. Seven rhi-

some systems had as a contrast, been grazed only in 1978 and three systems in 1982. Figures 8a & 8b illustrate the same phenomenon but here no relationships were studied between the shoot systems.

Table 3 shows how a fraction of the cut biomass of the dwarf shrubs was consumed when small rodents grazed in the subnival cavity. Much material was left cut and dying under the snow. Especially shoots of Empetrum were largely cut and left in the snow by rodents biting the lower parts. In comparison with the other species, the largest part of the cut biomass of V. myrtillus was consumed, however.

In this respect V.vitis-idaea was intermediate between the above mentioned species.

3.3 The development of the vegetation after grazing

For a few weeks after the start of the growing season the grasses were favoured and multiplied in the previously grazed areas (Figs 5 & 6). During the next year Vaccinium myrtillus also increased its abundance but appeared to decline slightly after 2 years. Vaccinium vitisidaea reacted in a similar way as V. myrtillus but took longer to reach its optimum extent.

Finally, Empetrum hermaphroditum took at least four years to recover from the effects of severe grazing (Fig 6). If the grazing had been less extensive it recovered faster (Fig. 5) but then there was also a tendency for the species to vary in cover during the years after the grazing had taken place.

3.4 Variations in rodent density in the study area

The breeding success of species such as the snowy owl, long-tailed skua and rough-legged buzzard (Andersson, unpubl.data.) indicated that the population density of the rodents was greatest in the years 1974, 1978 and 1982, but the indications for 1974 and 1972 are not as strong as for 1978. The density of faeces during 1978/79 and 1980/81 (Table 7) also indicated the

variations in rodent populations in the investigation plots.

3.5 Grazing preference experiments (Table 8)

Vaccinium myrtillus was one of the more common plants on the investigation plots and was eaten with greatest preference by Clethrionomys rufocanus. Linnaea borealis was eaten only slightly by the rodents and Sphagnum spp. was not eaten at all.

4 DISCUSSION

4.1 The relevance of the methods

The investigation plots for determining the regional distribution of grazing and the grazing along the slopes could not be located entirely at random because of transportation problems and because of difficulties in finding areas of the predetermined vegetation type. The method used certainly resulted in an underestimation of the grazing effects, as plots grazed less than 50% (see 2.1 B) were not considered. However, the large relative difference in grazing pressure within the whole region is nevertheless striking.

The extent to which the herbivory described in this paper occurred during winter is questionable. Most of the grazing of Empetrum hermaphroditum, however, should have taken place in the winter as most of the loose fairly fresh tops of Empetrum shoots which were found correlated well with the ends of the shoots remaining in the ground.

In the present paper, great emphasis is placed on the detailed study of the 3-4 most common vascular plants in the vegetation. Consequently, it was not possible to use conventional cover values in, for example, 1 m² squares, since they yield too little detailed information. Instead, such detailed information was collected at site b where 25 dm² plots

were divided into 400 smaller plots (See Table 2,8). However, it is possible to use cover values when describing grazing in more general terms. Ericson (1977) estimated cover and frequency in 1 m^2 plots but used 'individual counting' in plots of $1/16 \text{ m}^2$. He was, therefore, able to study the life spans of individual shoots of Vaccinium vitis-idaea, V. myrtillus and Empetrum hermaphroditum. This 'individual counting' method has great advantages for the Vaccinium species. In the Torneträsk area, however, it was not possible to determine the age of of Vaccinium shoots. Moreover, the method was not applied to Empetrum in the Torneträsk area since tests with marking individual shoots resulted in damage to the shoots. In the present paper, the detailed studies were therefore carried out only in the 25 dm^2 plots sub-divided into 400 smaller plots.

For precise and detailed studies of the population dynamics of the dwarf shrubs, neither the individual marking approach nor the method used here, based on 400 small subplots, is totally adequate. Neither method gives information on the inter-relationships between individual aerial shoots. In some cases, shoots occurring close together may arise from close positions on a common rhizome whereas in other cases closely associated shoots may belong to different rhizome systems. If a shoot is damaged, other shoots attached to the same rhizome system may also be affected, whereas a shoot from another rhizome occurring close to the damaged shoot will be unaffected. This has been demonstrated for Vaccinium vitis-idaea (Karlsson and Emanuelsson, in prep). Thus, for better predictions of the reaction of a population of shoots to grazing, the relationships between individual shoots must be known. An attempt to solve this problem is described briefly in section 2.2.7. The objective of this pilot investigation was to follow a shoot population and then excavate the rhizome system to establish the inter-relationships between the shoots. As there was a limited number of permanent plots for investigating the grazing by rodents in this investigation, only a few were used for this type of inter-relationship studies as it is a destructive method.

4.2 The dynamics of the rodent grazing

Direct investigations of the number of small rodents in the Torneträsk area during the investigation period could not be carried out. Their abundance was, however, estimated indirectly. The number of droppings collected from some sample plots (2.1.4) indicates peak populations of rodents in 1977/78 and to a lesser degree, in 1981/82 (Table 6). Larsson (1978) quotes rodent population maximum in 1974 around Abisko and predicted one for 1978. Ericson (1977) also described a population maximum in 1973/74 in the Västerbotten area and Oksanen & Oksanen (1981) described a similar situation in 1977/78 for the Kilpisjärvi area of north-west Finland. The number of birds of prey and owls in the Torneträsk area also indicates population maxima for the rodents in the years 1977/78 and 1981/82 (Andersson, unpubl. data).

In the investigation area, almost all of the observations have been on Clethrionomys rufocanus. Very few observations of Lemmus lemmus were obtained and then mainly in the areas north of the Torneträsk. Clethrionomys rufocanus appears to dominate to the exclusion of Lemmus lemmus. Larson (1978) also shows that C. rufocanus is totally dominant in the Empetrum-dominated vegetation type of the Torneträsk area. It can be assumed, therefore, that C. rufocanus was responsible for most of the grazing in the sample plots during the winter of 1977/78.

Kalela (1958) describes Clethrionomys rufocanus as a species which will not eat Empetrum if herbs and Vaccinium myrtillus are available as alternatives. The present investigation confirms this (Table 8).

The intensive grazing described in the present paper contrasts somewhat with the situation described by Kalela (1958) and Ericson (1977). It seems, therefore, that Empetrum hermaphroditum is grazed under the snow in years when food is particularly limited to the rodents. The same seems to be partially true for Vaccinium vitis-idaea whereas V. myrtillus, a

preferred food, is also eaten during summer (Oksanen & Oksanen 1981). In addition, the numbers of detached stems found in the spring do not correlate with the numbers of cut stems remaining in the ground. It may be concluded, therefore, that Empetrum and V. vitis-idaea are greatly affected by rodent grazing only during the winters of years when alternative food is sparse. The grazing of V. myrtillus is not, however, restricted to the winter.

Tast & Kalela (1971) mention C. rufocanus as a herbivore which seldom grazes below the soil surface. An investigation by Kalela (1957) on its food preferences shows that it foremost prefers Vaccinium myrtillus and then, in order, V. vitis-idaea, V. uliginosum, Empetrum hermaphroditum, Linnaea borealis and Betula nana. The food preference experiment presented here is less extensive than Kalela's (1957) investigation but a similar order was found except that V. vitis-idaea was grazed less in the present trial. This could be explained by assuming that the rodents in the present study might have been given shoots of V. vitis-idaea from newly grazed rhizome systems. Other results in this investigation indicate that grazing can induce a "defence reaction" in V. vitis-idaea; newly grazed rhizome systems being unpalatable to the rodents. The rodents' low preference for Linnaea borealis is shown in the present investigation and also by Kalela (1957): the results for the grasses and mosses also approximately agree between the two studies.

In the field, the food preferences vary from those determined in the cage experiments. The results from Abisko indicate that Empetrum hermaphroditum and Vaccinium vitis-idaea are grazed to a greater extent in the winter than would be expected from the results of the food preference studies. However, the preferences vary greatly (Figs. 6 and 7 and Table 3). Kalela (1957) shows a lower degree of grazing of Vaccinium vitis-idaea than was expected from his food preference studies.

It is probable that most of the grazing around Abisko described in this investigation took place during the winter of 1977/78 as there are striking reductions in the abundance of most of the species after this winter (Fig. 5). Vaccinium

myrtilus appears to be grazed to some extent even during the summer, e.g. 1978 (Fig. 5). This must be due to its great productivity.

The large regional differences in the intensity of winter grazing (Fig. 3) cannot be fully explained. Measurements of snow depth and consistency in all of the sample areas were not carried out but the obvious geographical trend over the whole area suggests that meteorological factors are the main reason for the variation. Climatological conditions, but on a small scale, may also explain the differences found in winter grazing along the slopes in the birch forest around Abisko. On these slopes, the tops of small hills probably have so little snow in winter that a sub-nival space cannot develop. At the bottom of the slopes, the snow may be particularly deep and water which accumulates here may freeze and prevent the development of a sub-nival space also here. Elsewhere along the slopes, however, the conditions may favour the development of a sub-nival cavity and the grazing will then be concentrated to these areas.

In comparison with the findings of other investigators (Ericson, 1977; Kalela, 1958; Kalela et al., 1971), the winter grazing described in this paper seems to have been particularly extensive. Much of the impact on the dwarf shrubs has been found to result from shoot death after cutting by the rodents rather than by direct consumption. This phenomenon does not seem to have been previously described. The death of bitten but unconsumed shoots was also observed after the winter of 1981/82 in many of the dwarf shrubs heaths in the Abisko area. Empetrum had the lowest proportion of dead phytomass that had been eaten rather than just cut. Kalela (1958; Kalela et al., 1971) only mentions that rodents eat leaves and not stems. Neither Ericson (1977) nor Oksanen & Oksanen (1981) stress the presence of remaining vegetation cut by the rodents.

This effect of grazing and leaving dead shoots was observed by the present author in the Kilpisjärvi area in 1978 although less pronounced than in the Abisko area.

Excavations in the Njoutjousvagge area during the early spring of 1982 showed that shoots of the dwarf shrubs which had been detached by the rodents could only be found if an ice layer had developed above a loose snow layer 2 to 7 cms deep. If this loose snow layer did not occur, there was no grazing outside the well established runways created by the rodents. If the ice layer was absent, no detached shoots of the dwarf shrubs were to be found. These circumstances suggest that warm weather in periods of the early winter can enable this type of grazing to occur especially in places with relatively much snow. During such mild weather and during periods of alternating warm and cold weather an ice layer may form directly on the vegetation in places with less snow, which makes the lower parts of the plants inaccessible to the rodents. A similar phenomenon may also explain why there is no grazing at the bottom of the slopes in the birch forest where water can accumulate during mild periods and then in cold periods freeze solid.

The occurrence of instable temperature conditions in winter may concentrate individuals of small rodents in those areas where winter grazing is possible. The voles may even be driven out of other vegetation types by unfavourable snow conditions. In years with high population densities, interspecific competition may also force some species into less favourable vegetation types (cf. Larsson, 1978). In years when high population densities of rodents combined with weather conditions which create ice layers at the ground surface, individuals of, e.g., Clethrionomys rufocanus may concentrate on areas of Empetrum where the ice layer often forms some centimeters above the ground surface.

A visual inspection of these areas indicates that few defined runways exist where the rodents have grazed. This contrasts with Ericson's (1977) observations of many runways. This difference may be attributed to differences in snow conditions and as well as the lack of Myopus schisticolor in the Torneträsk area which often creates runways (Ericson 1977). Following the grazing described in the Torneträsk area, the recolonization by dwarf shrubs appears to take place totally by

vegetative proliferation as seedlings were absent.

In areas where Vaccinium myrtillus is common, the vegetation is more palatable to the voles (Table 5) and will be grazed. The investigations showed that V. vitis-idaea grazed once will probably not be grazed again for several years (Fig. 7a & 7b). The observations of rhizomes of V. vitis-idaea in areas which have been grazed many times suggest the existence of a "defence system" which may be similar to the chemical defence system described in Betula pubescens by Haukioja (1980). Also, Oksanen & Oksanen (1981) has found high concentrations of phenols in V. myrtillus in years following grazing. The extent to which chemical defence mechanisms can be induced in Betula pubescens decreases from sub-arctic to temperate regions (Haukoja 1980). Haukoja (1980) hypothesizes that the mass occurrence of Oporinia autumnata may be one factor which induces better chemical defence systems in Betula pubescens from sub-arctic areas. A similar response to rodent grazing may occur in V. vitis-idaea.

4.3 The dynamics of the vegetation

In general, the variation in the vegetation presented here is very similar to that described by Ericson (1977) after a rodent grazing year. However, in the present investigation, Empetrum hermaphroditum had a cover of between 30 and 60% whereas it was only about 1% in Ericson's study. After peak grazing intensity (probably in the winter of 1973/74 in Ericson's study; 1977/78 in the present investigation), grasses and shrubs were shown to diminish in both studies. However, grasses then recovered faster in the present study than in that by Ericson (1977). In the Abisko area, the grasses, particularly Deschampsia flexuosa, had already begun to decline by the late summer of 1979 whereas they were continuing to grow 3 years after grazing in Ericson's study. Oksanen (1981) reported an opposite trend whereby the exclusion of rodents favoured the increase in abundance of graminoids. However, the vegetation studied by him was slightly different, more dominated by grasses and herbs.

In the present investigation, Vaccinium myrtillus appears to recover as fast as the graminoids but then maintains a great abundance for the rest of the investigation. The contrasting prolonged decrease in the abundance of V. myrtillus found by Ericson (1977) was, perhaps, the result of caterpillar grazing (Ericson, pers. comm.). Vaccinium myrtillus was much more important in the vegetation studied by Oksanen & Oksanen (1981) and it expanded after grazing, particularly in areas where rodents were subsequently excluded.

The differences between the Vaccinium species and Empetrum in their abilities to recolonize an area vegetatively, may probably be explained by the fact that comparatively similar grazing by small rodents has different effects on the two taxa.

The inability of Empetrum to produce new shoots on old stems will result in a lack of reserve buds able to develop after the current year's shoots have been grazed. The species must, therefore, invade grazed areas from peripheral areas by the growth of new branches which produce adventitious roots (Figs. 7A & B). In contrast, the Vaccinium species can recolonise from the development of buds on the rhizome or, in V. myrtillus, even cut aerial shoots are able to regenerate. As a result of these circumstances, the Vaccinium species gain a large competitive advantage in the dwarf shrub vegetation in the years following heavy rodent grazing.

The effect of this phenomenon will be even more visible as no seedlings seem to occur in grazed areas where there are few and indistinct runways. These seedlings could have provided a good recolonization source for Empetrum. In the Torneträsk area, it is obvious that the grazing in the period 1977 to 1982 has favoured the growth of the Vaccinium species to the detriment of Empetrum.

It is probable that the grazing also exerts a diversifying effect on the vegetation and this is sometimes more obvious in coniferous forests where non-clonal plant species depending on seeds are more common (Ericson 1977). In general, it is difficult to predict the long term-dynamics of the Empetrum-dominated vegetation in arctic and sub-arctic ecosystems in

relation to rodent grazing. In fact, data presented in this paper support the theory that the rodent grazing diversifies the dwarf shrub vegetation. Also, in the mid-alpine region, at least that in the Abisko area, there appears to be much less rodent grazing but more pronounced dominance of the dwarf shrub species in these areas, and abiotic factors seem to have a more important effect on the differentiation of the vegetation. It is interesting that Vaccinium uliginosum in these areas grows with very little snow cover whereas it is absent from similar sites at lower levels where it is probably grazed to extinction (compare Fig. 4a-c). It has also been shown that V. uliginosum is even slower than Empetrum to recolonise previously grazed areas (Emanuelsson, 1984 b).

However, the existence of less grazing activity at higher altitudes as well as the existence of larger unbroken patches of dwarf shrubs is still not well supported by hard data.

Finally, other types of herbivory may have similar effects on the vegetation as those of the rodents on the dwarf shrub heaths. Sandberg (1958), describing the total destruction of the dwarf shrub vegetation by Epirrata autumnata in the birch forest of the Abisko area, states that grasses and Linnæa borealis were most favoured by the Epirrata grazing. Vaccinium vitis-idaea and V. myrtillus were probably also favoured by the Epirrata whereas Empetrum would experience more difficulties in recolonising. But, it should be noted that Epirrata grazing in the field- and bottom-layer takes place much more seldomly (approximately every 40 years according to Tenow (1975)) than heavy small rodent grazing.

Compared to other factors, rodents seem to have a significant role on the dynamics and performance of the Empetrum vegetation in the Abisko area. But how large is this role in relation to the other factors?

Traditionally, abiotic factors such as nutrient levels, soil water and snow cover have been stressed when explaining the distribution of dwarf shrubs in arctic and subarctic environ-

ments. But, we still know too little about the Empetrum dominated vegetation to be able to compare and distinguish between abiotic factors, grazing factors and competition from other plants. Some notes, however, may be proposed in this field.

In the Scandinavian mountain range the Empetrum vegetation is considered to be restricted to areas with poor or moderate snow cover (Nordhagen, 1943; Du Reitz, 1950; Sjörs, 1956; Hämet-Ahti, 1963; Gjaerevoll, 1965; Sonesson, 1969; Sonesson & Lundberg 1974). Vaccinium vitis-idaea is found in areas with little snow cover while Vaccinium myrtillus is significant in the vegetation if the snow cover is thicker.

The zonation found in many snow beds on poor soils in the low alpine belt also indicates that Empetrum hermaphroditum and Vaccinium vitis-idaea are favoured by little snow cover while Vaccinium myrtillus occurs lower down in the snow bed where the snow cover is deeper (Gjaerevoll 1965, Sonesson 1969, Wijk 1980).

Gjaerevoll (1965) discusses the differences in growing season and ability to be dried out in the spring as the differentiating factors in snow beds. The results presented here, showing great differences in rodent winter grazing depending upon the snow cover, do not directly contradict such assumptions but show that winter grazing by rodents may, to some extent, be the vector whereby winter snow cover differentiates the composition of the dwarf shrub communities. Also it can be assumed that in intermediate vegetation types where Empetrum and Vaccinium myrtillus coexist, this may largely be a result of influence of rodents. With respect to grazing in the intermediate vegetation types, one can assume that Empetrum should have been much more dominant if grazing had not occurred. The grazing seems to 'move' the limits between places where Empetrum is dominant and where Vaccinium myrtillus is dominant. The grazing also seems to make it possible for grasses to occur in the dwarf shrub communities by giving them the opportunity to develop rapidly after the dwarf shrubs have been cut.

Similarly, the winter grazing by small rodents can perhaps change the limits between dwarf shrub communities and meadow communities in favour of the latter.

For example, it is often assumed (see e.g. Sjörs 1956) that the dwarf shrub communities were limited at higher altitudes by the soil movements due to frost, and substituted by grass heaths. Perhaps the limits for the grass heaths can be expanded by the grazing of the rodents.

In a similar way, dwarf shrub communities and herb meadows are found in a mixture on the mountain slopes. The occurrences of herb meadows are usually explained by the influence of moving soil water (Sjörs, 1956; Sonesson and Lundberg, 1974). Possibly, such meadows can expand in years after rodent grazing as the grazing largely restrains the growth of Empetrum and to some extent the Vaccinium species.

The large scale differentiation of the Empetrum-dominated dwarf shrub heaths may mainly be controlled by abiotic factors such as ground water, snow depth, frost, dryness in spring and frost-heaving, especially in the mid-alpine region (Gjærevoll, 1965; Sjörs, 1972; Sonesson and Lundberg, 1974). However, biotic influence from grazing and trampling animals, may be very important as well, especially for the detailed differentiation and dynamics of the vegetation.

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5. REFERENCES

- van den Brink, F.H. 1958. Alla Europas däggdjur. - Stockholm.
- Coulianos, C-C. and Edström, R. 1971. Djuren, växterna och vintern. - Svenska Naturskyddsföreningen, 76 pp.
- Du Reitz, G.E. 1950. Phytogeographical excursion to the surroundings of Lake Torneträsk in Torne Lappmark (northern Sweden). - 7th Int. Bot. Congr., Stockholm 1950. Excursion guide CIIIC, 19pp.
- Emanuelsson, U. 1984a. Short-term effects of trampling in subalpine and alpine ecosystems in the Torneträsk area, northern Sweden. Dept. of Plant Ecology, Univ. of Lund (Manuscript).
- Emanuelsson, U. 1984b. Vegetation zonation on tracks through dwarf shrub heaths in the Torneträsk area, northern Sweden. Dept. of Plant Ecology, Univ. of Lund (Manuscript).
- Ericson, L. 1977. The influence of voles and lemmings on the vegetation in a coniferous forest during a 4-year period in northern Sweden. Wahlenbergia, vol. 4.
- Flower-Ellis, J.G.K. 1971. Age structure and dynamics in stands of bilberry (*Vaccinium myrtillus* L.). Rapporter och uppsatser. Avd f skogsekologi. Skogshögskolan. Stockholm 9:1-108.
- Gjaerevoll, O. 1965. Plant cover of the alpine region.- Acta Phytogeographica Suecica 50. p. 255-268.
- Golley, F.B., Ryszkowski, L. & Sokur, J.T. 1975. The role of small mammals in temperate forests, grasslands and cultivated fields. In: Small mammals: their productivity and population dynamics (ed. F.B. Golley, K. Petrusewicz & L. Ryszkowski). Intern. Biol. Programme 5:223-241. Cambridge University Press. Cambridge.
- Haukioja, E. 1980. On the role of plant defences in the fluctuation of herbivore populations. Oikos 35:202-213.

- Haukioja, E., Kapiainen, K., Niemelä, P. & Tuomi, J. 1983. Plant availability hypothesis and other explanations of herbivore cycles: complementary or exclusive alternatives? - *Oikos* 40:419-432.
- Helle, T. and Aspi, J. 1983. Effects of winter grazing by reindeer on vegetation. - *Oikos* 40:337-343.
- Hultén, E. 1950. Atlas över växternas utbredning i Norden. - Stockholm.
- Hämet-Ahti, L. 1963. Zonation of the mountain birch forest in northernmost Fennoscandia. *Ann. Bot. Soc. "Vanamo"* 34 (4), 127 pp.
- Kalela, O. 1957. Regulation of reproduction rate in subarctic populations of the vole *Clethrionomys rufocanus*. *Ann. Acad. Sci. Fennicae A IV Biol.* 34:1-60.
- Kalela, O., Kilpeläinen, L., Koponen, T. & Tast, J. 1971. Seasonal differences in habitats of the Norwegian lemming, *Lemmus lemmus* (L.), in 1959 and 1960 at Kilpisjärvi, Finnish Lapland. *Ann. Acad. Sci. Fennicae A IV Biol.* 178:1-22.
- Krok, T.O.B.N. & Almquist, S. 1962. Svensk flora för skolor. Kryptogamer. 25 uppl. - Stockholm.
- Larsson, T-B. 1978. Smågnagarstudier i Torne träskområdet 1974. *Fauna och Flora* No. 1 1978.
- Lid, J. 1974. Norsk og svensk flora. 2 uppl. - Oslo.
- Nordhagen, R. 1943. Siklisdalen og Norges fjellbeiter. - *Bergens Mus. Skr.* 22, 607 pp.
- Oksanen, L. and Oksanen, T. 1981. Lemmings (*Lemmus lemmus*) and grey-sided voles (*Clethrionomys rufocanus*) in interaction with their resources and predators on Finnmarksvidda northern Norway. - *Rep. Kevo Subarctic Res. Stat.* 17:7-31.
- Sandberg, G. 1958. Fjällens vegetationsregioner, vegetationsserier och viktigaste växtekologiska faktorer. pp. 36-60. In: Skuncke, F. (ed), 1958. Renbeten och deras gradering. Lappväsendet - Renforskningen, Medd 4, Uppsala. 204 pp.
- Schultz, A.M. 1964. The nutrient-recovery hypothesis for Arctic microtine cycles. II. Ecosystem variables in relation to Arctic microtine cycles. In: *Grazing in Terrestrial and Marine Environments* (ed. D. Crisp) pp. 57-68. Blackwell's. Oxford.

- 1969. A study of an ecosystem: the Arctic Tundra pp. 77-93.
In: The Ecosystem Concept in Natural Resource Management
(ed. G.M. Van Dyne). Academic Press. New York & London.
- Sjörs, H. 1956. Nordisk växtgeografi.
Stockholm.
- Sonesson, M. 1969. Studies on mire vegetation in the Torneträsk area, northern Sweden.
II Winter conditions of the poor mires.
Bot Notiser 122:481-511.
- Sonesson, M. & Lundberg, B. 1974. Late Quaternary forest development of the Torneträsk area, North Sweden. I. Structure of modern forest ecosystems. Oikos 25:121-133.
- Tast, J. & Kalela, O. 1971. Comparisons between rodent cycles and plant production in Finnish Lapland. Ann. Acad. Scient. fennicae A IV Biol. 186:1-14.
- Tenow, O. 1975. Topographical dependence of an outbreak of *Oporinia autumnata* Bkh. (Lep., Geometridae) in a Mountain Birch Forest in Northern Sweden. Zoon 3:85-110.
- Teär, J. 1972. Vegetativ och fruktativ utveckling hos viltväxande och odlade lingon. Lantbrukshögskolan, Diss. 79. 110 pp.
- Warming, E. 1908. The structure and biology of arctic flowering plants. I. Ericineae. Medd. om Grönland 36.
- Wijk, S. 1980. Växterna och snötäcket. Fauna och Flora No.1 1980.
- Vegetationskartor över svenska fjällkedjan. 1979-84. Liber Kartor, Stockholm.

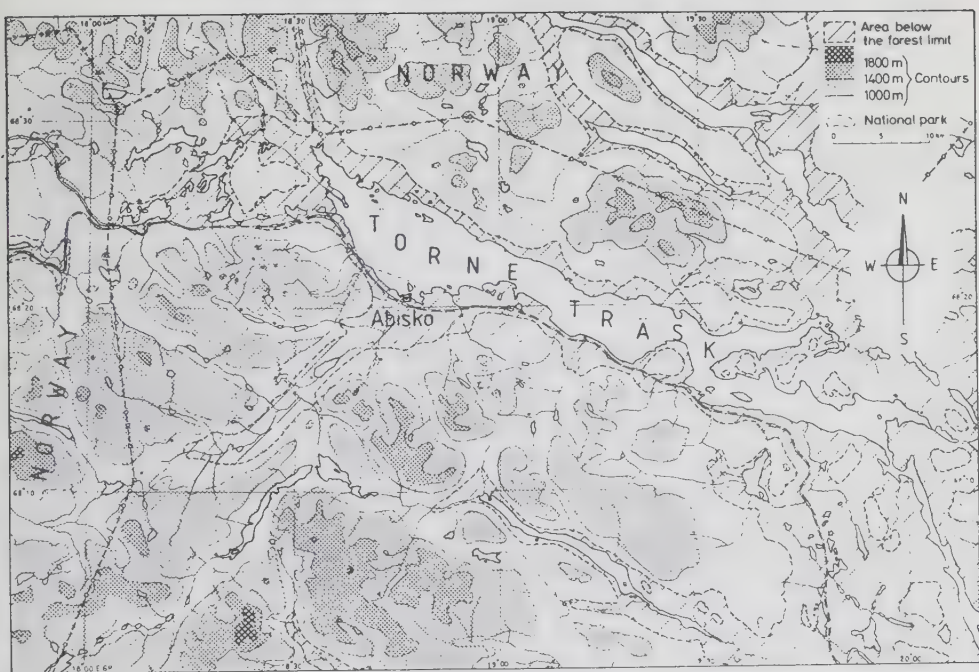


Fig 1a.
Map of the Torne-träsk area (adapted from Sonesson & Lundberg 1974).----- = tree-line.

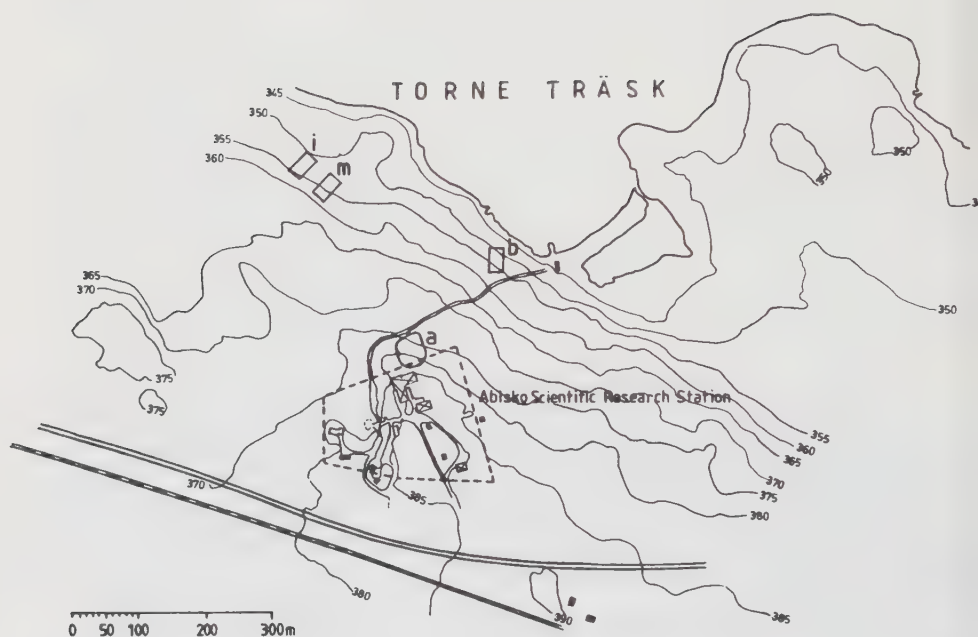


Fig 1b.
Main sites a,b,i and m at Abisko. Cf. Table 1, 2 and text.



Fig 2a.

Illustration of how a number of vascular plants grow in Empetrum hermaphroditum dominated vegetation around Abisko.

A. Empetrum hermaphroditum depends to a large extent upon aboveground shoots for its clonal growth. Older living parts of the plant are found quite deep in the peaty soil. This is due to the covering of these parts by continuous litterfall.

B. Vaccinium vitis-idaea has an extensive rhizome system with a bud-bank. From these buds new shoots can develop but often the shoots are terminal parts of the rhizome.

C. Vaccinium myrtillus has a shallower rhizome system than V. vitis-idaea. Buds both on the rhizome and on vertical shoots are capable of developing into a shoot.

D. Vaccinium uliginosum has a rhizome system but expands often also by branches that are bent down and covered by litter.

E. Calamagrostis lapponica has an extensive rhizome system with numerous dormant buds capable of developing into aboveground shoots.



2b. Illustration of how dwarf-shrub vegetation is grazed during winter.

1. *Empetrum hermaphroditum* 2. *Vaccinium myrtillus* 3. *Vaccinium vitis-idaea* 4. *Calamagrostis lapponica* 5. Top shoots of *Vaccinium vitis-idaea*, *V. myrtillus* and *Empetrum hermaphroditum*, not available to grazing as they are frozen into the compact snow layer 6. Snow 7. Ice layer 8. Sub-nivale space 9. Grazing *Clethrionomys rufocanus* 10. Peaty soil 11. Mineral soil 12. Border between mineral and peaty soil 13. Older parts of *Empetrum hermaphroditum* which has lost its younger shoots



2c. The same site as in Fig. 2b during the subsequent spring.
 1. Empetrum hermaphroditum 2. Vaccinium myrtillus 3. Vaccinium vitis-idaea 4. Calamagrostis lapponica 5. Dead top shoots which were not available to the rodents as they had been frozen into the compact snow layer 6. Peaty soil 7. Mineral soil 8. Border between mineral and peaty soil 9. Older parts of Empetrum hermaphroditum which has lost its younger shoots

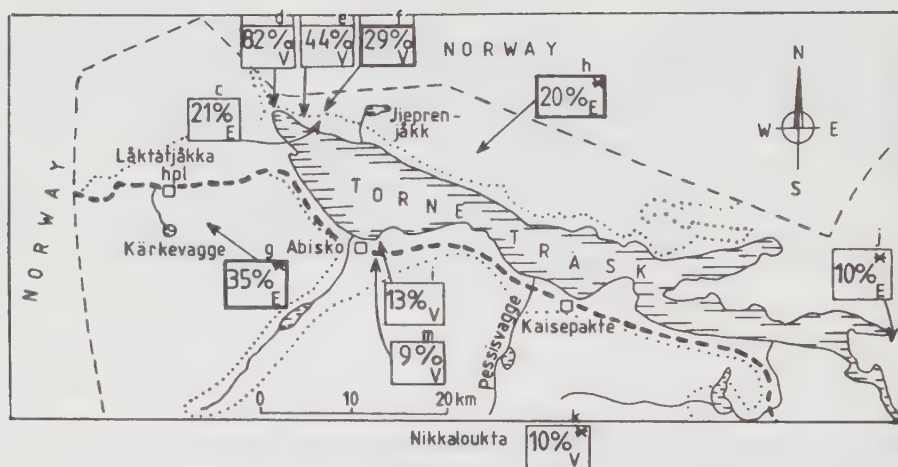


Fig 3.

Grazing by rodents at nine sites (c-j,m) in the Torneträsk area and one at Nikkaloukta (k) during the winter of 1977/78. Percentage of grazed plots shown, i.e. those estimated to have lost 50% or more of their phytomass within each site investigated in 1978, above (sites marked with thick frames) and below (thin frames) tree-line (dotted line). Number of plots at each site was 4250 (1 dm²).

Asterisks mark sites where a less detailed method was used (200 plots/site).

E=Empetrum type; V=Empetrum-Vaccinium myrtillus type.

4 a.

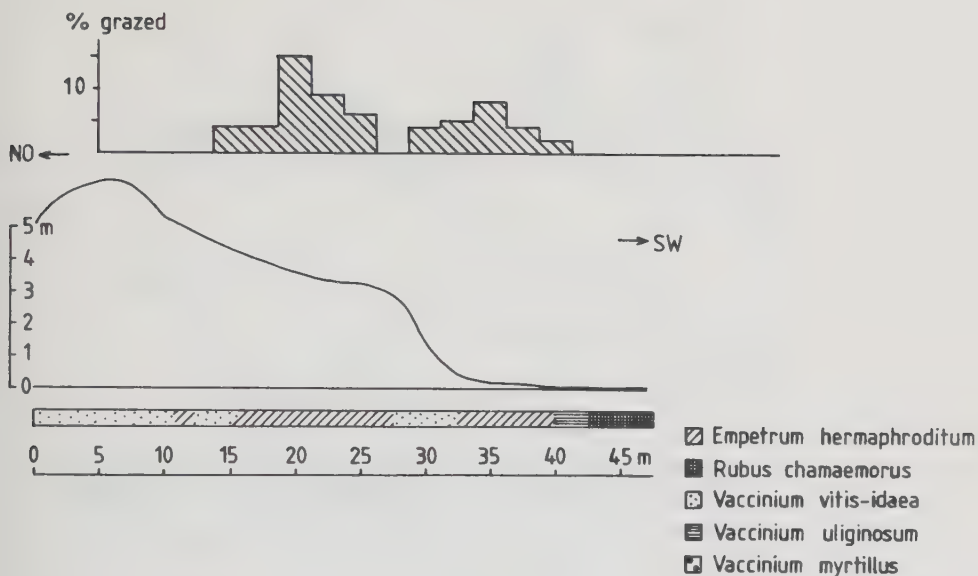
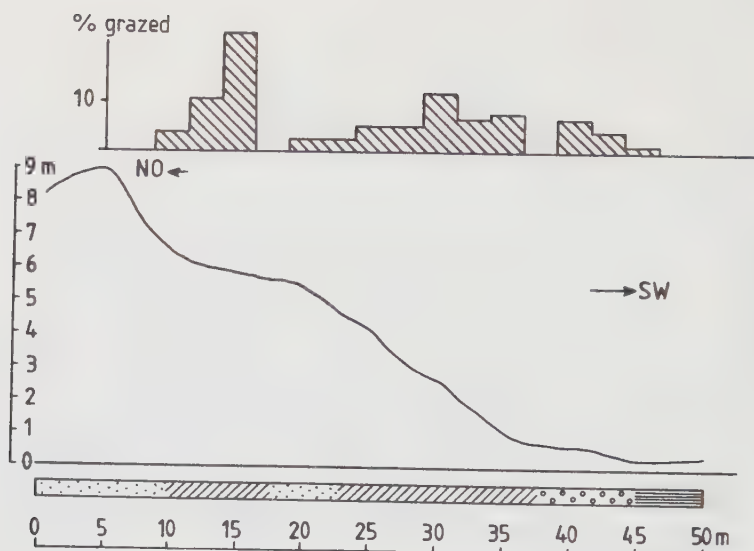


Fig 4 a-c.

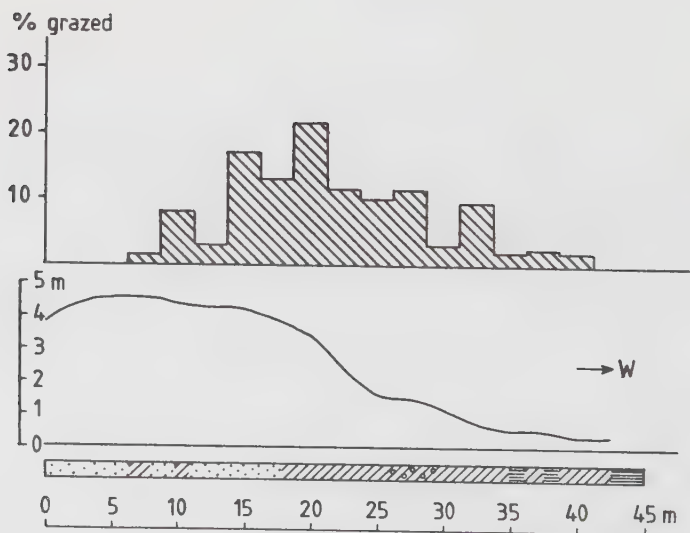
Percentage of plots (1 dm²) grazed to 50% or more along three slopes with vegetation zonation characterized by five species. Along each slope a 2.5 m wide transect was studied. The transects measured approximately 50 m in length. At every meter along the transects 50 plots were investigated.

The slopes were situated 500-800 m SSW from Abisko Scientific Research Station at approximately 450 m altitude.

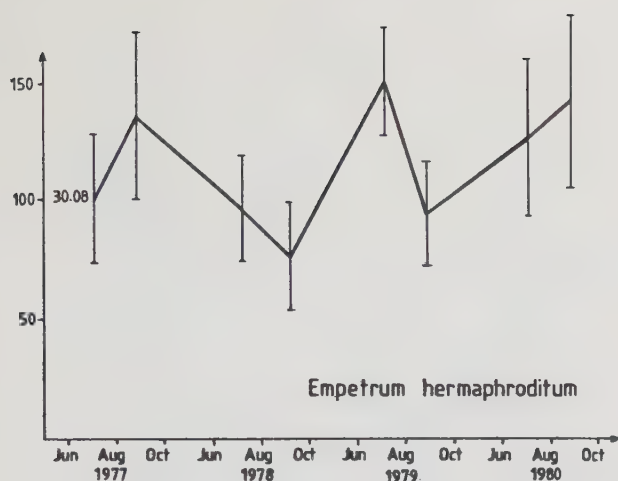
4b.



4c.



5a



5b

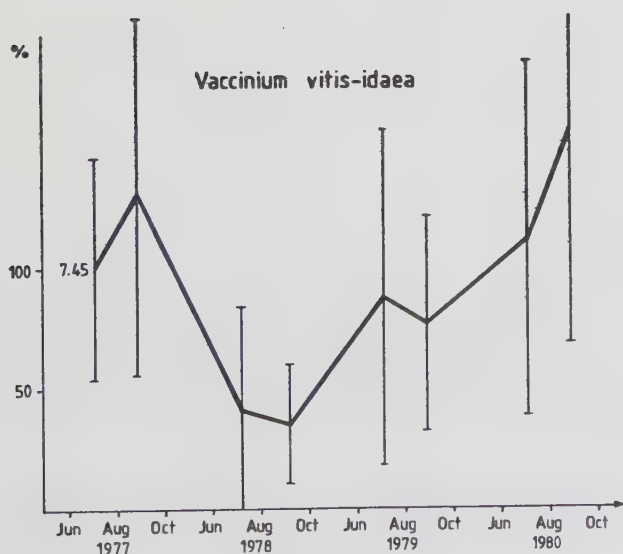
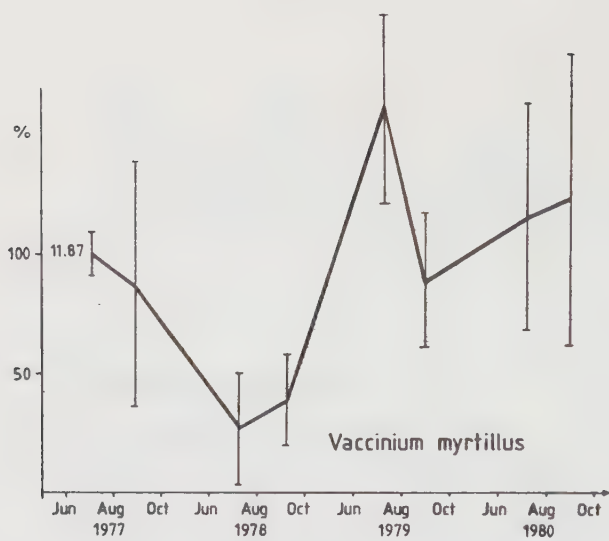


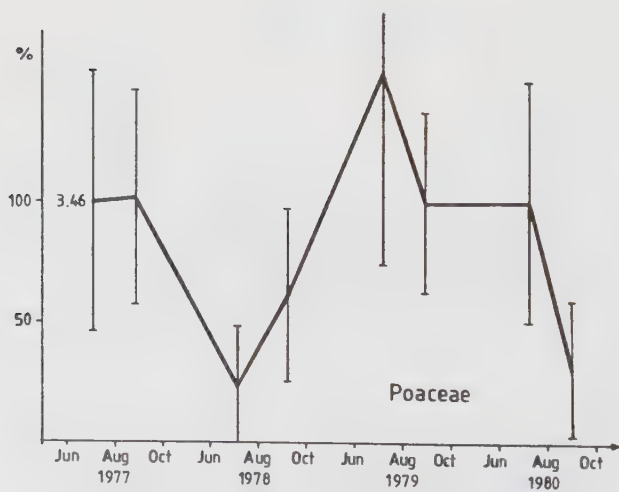
Fig 5 a-d.

Mean percentage cover ($n=128$) of three dwarf shrubs and grasses from June 1977 to August 1980 at a site near Abisko Scientific Research Station (site a in Fig 1b). Bars represent standard deviation. The numbers at the beginning of the diagrams show the absolute cover at the beginning of the investigation.

5c



5d



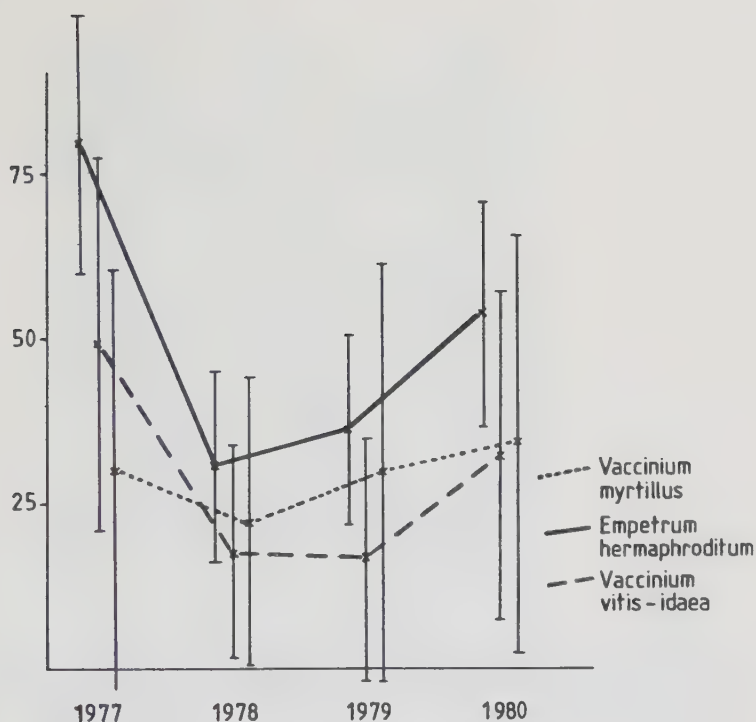


Fig 6.

Mean frequency of some species inside 15 25dm² plots (Table 2,B) during the period 1977-1980. Each plot contained 400 sub-plots where presence or absence was recorded. All 15 plots were chosen in 1978 since they seemed to have been grazed during the winter 1977/78. The values for 1977 are reconstructed on the basis of cut stems found in spring 1978.

Fig. 7a

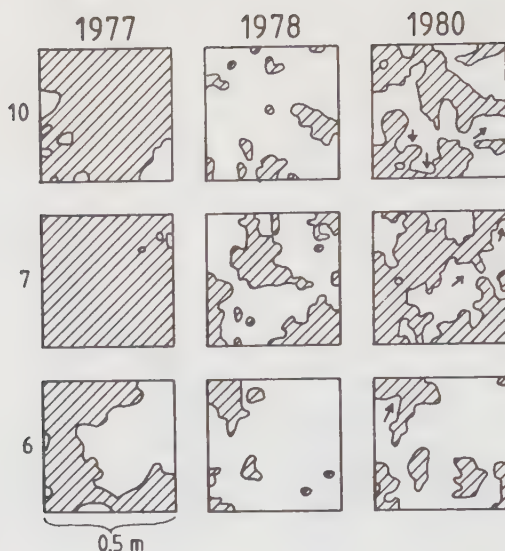


Fig. 7b

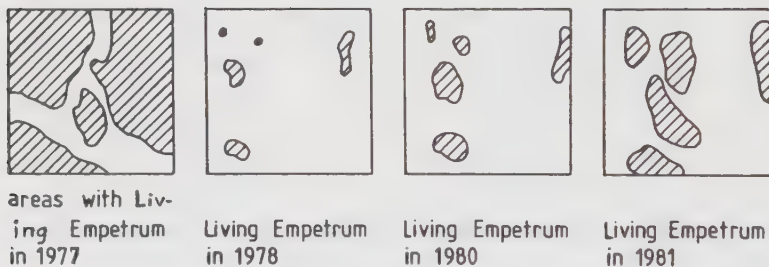


Fig 7 a-b.

Maps of the green parts of *Empetrum hermaphroditum* in 3 of the 15 investigation plots (7a) described in the legend of Fig. 6. Arrows in Fig. 7a show where the green parts of *Empetrum* were not found in 1980 although found in 1978.

Fig. 7b illustrates a separate investigation plot close to site b. The "movement" of the green parts of *Empetrum* over the ground can be clearly seen.

Vaccinium vitis-idaea

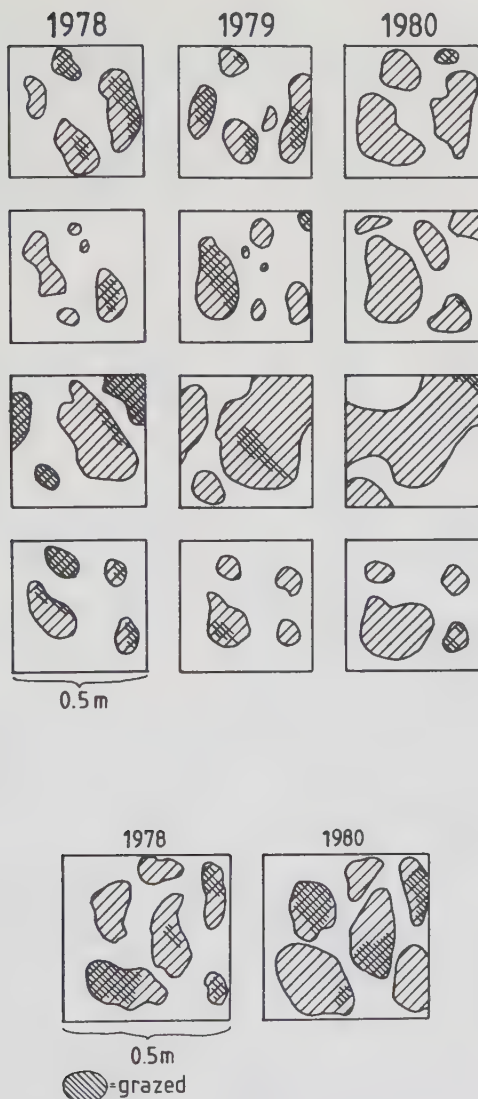


Fig 8.
The cover of *Vaccinium vitis-idaea* in five plots during three years. The figure shows that the same parts were grazed only rarely on two consecutive occasions. If the figure had been based on an area where *V. vitis-idaea* is less common, the tendency would not have been so clear.

Table 1.

Species composition in the vegetation types described by Sonesson & Lundberg (1974) as "Empetrum-type" (column 1) and "Empetrum-Vaccinium myrtillus-type" (column 2). Frequencies in percent and characteristic cover as defined by Malmer (1962).

Columns 3-4 show mean cover in percent and standard deviation or only presence (+) in similar sites (3=site A, 4=site B) investigated by the present author (cf. Fig 1b). See further text; 2.1.

	1	2	3	4
<i>Empetrum hermaphroditum</i>	100 ⁵	100 ⁴	30+-9	80+-20
<i>Vaccinium myrtillus</i>	52 ¹	100 ⁴	11,9+-1,1	30+-30
<i>Vaccinium uliginosum</i>	24 ²	20 ¹	+	+
<i>Vaccinium vitis-idaea</i>	100 ²	70 ²	7,5+-3,5	49+-23
<i>Calamagrostis lapponica</i>	-	-		
<i>Deschampsia flexuosa</i>	52 ¹	100 ¹	4,5+-1,9	+
<i>Festuca ovina</i>	90 ¹	10 ¹		
<i>Arctostaphylos alpina</i>	29 ³	-		
<i>Chamaenerion angustifolium</i>	5 ¹	-	+	
<i>Cornus suecica</i>	5 ¹	-		
<i>Linnaea borealis</i>	76 ¹	30 ¹	+	+
<i>Luzula pilosa</i>	5 ¹	-		
<i>Melampyrum pratense</i>	19 ¹	40 ¹		
<i>Melampyrum silvaticum</i>	5 ¹	10 ¹		
<i>Pedicularis lapponica</i>	5 ¹	-	+	+
<i>Solidago virgaurea</i>	10 ¹	30 ¹	+	
<i>Trientalis europaea</i>	19 ¹	40 ¹	+	
<i>Equisetum pratense</i>	29 ¹	-	+	
<i>Equisetum silvaticum</i>			+	+
<i>Gymnocarpium dryopteris</i>	5 ¹	-		
<i>Lycopodium annotinum</i>	10 ¹	10 ¹		
<i>Cladonia elongata</i>	52 ¹	90 ¹	+	+
<i>Cladonia rangiferina</i>	52 ¹	50 ¹		
<i>Cladonia silvatica</i>	52 ¹	40 ¹		
<i>Nephroma arcticum</i>	38 ²	50 ¹	+	+
<i>Peltigra aphthosa</i>	24 ¹	-	+	
<i>Peltigra polydactyla</i>	24 ¹	-		
<i>Stereocaulon paschale</i>			+	
<i>Barbilophozia lycopodioides</i>	24 ¹	100 ³	+	+
<i>Brachythecium reflexum</i>	29 ¹	-		
<i>Dicranum spp.</i>	86 ²	100 ³	+	+
<i>Hepaticae spp.</i>			+	+
<i>Hylocomium splendens</i>	52 ²	40 ¹	+	+
<i>Pleurozium schreberi</i>	81 ¹	100 ³	+	+
<i>Ptilidium ciliare</i>	52 ³	-		
<i>Polytrichum commune</i>	-	50 ³	+	+
<i>Polytrichum juniperinum</i>	67 ¹	60 ¹	+	+

Table 2.

Survey of the different investigations and experiments presented in this paper (cf text 2.1). The locations of the sites are shown in Figs. 1b and 3. Site 1 was located 500-800 m SSW of the Research Station.

Investigation/ experiment	Type of investigation/ experiment	Site	Type of plots
A	Investigation of long-term vegetational changes	a	8 plots with 16 sub-plots each plot: 5x0.6m sub-plot: 2.2dm ²
B	Investigation of detailed long-term vegetational changes	b	15 plots with 400 sub-plots each plot: 0.5x0.5 m sub-plot: 25x25mm
C	Regional patterns of winter grazing	c-k	each site con- tains 4250 1dm ² plots
D	Local grazing patterns	1	3 profiles 45-50 m x 2.5 m 500 1 dm ² sub-plot/m slo- pe
E	Estimation of grazed biomass	b	15 plots each 2.5 dm ²
F	Faeces countings	c,d	41 plots each 2.5 dm ²
G	Food preference studies		cages
H	Proportion of grazed species	b,i,m	500 1 dm ² /- site

Table 3.

Phytomass consumed by small rodents during the winter grazing of 1977/78. I, remaining detached stem parts; II, phytomass remaining intact above ground; III, estimated total above ground phytomass in similar ungrazed areas; IV, consumed phytomass: $IV = III - (I + II)$. The values derived from the relationship between shoot weight and leaf weight presented by Flower-Ellis (1971) are given in brackets.

	I g x m ⁻² +SD	II	III	IV
<i>Empetrum hermaphroditum</i>	29.6 +18.8	28.0 +17.6	approx. 100	approx. 32
<i>Vaccinium vitis-idaea</i>	13.2 +14.8	10.4 +14.4	approx. 50	approx. 26
<i>Vaccinium myrtillus</i>	6.0 +7.6 n=15	9.2 +8.8 n=15	approx.30 (34.8+46.8) n=15 (n=15)	approx.15 (19.6) n=15 (n=15)

Table 4.

The relationship between the grazed phytomass of four species in 15 0.5 x 0.5 m plots (site b). The table shows that it is only the pair *Empetrum hermaphroditum* - *Vaccinium vitis-idaea* which was simultaneously grazed to the same extent. $*=p^20.05$.

<i>Vaccinium myrtillus</i> - <i>V.vitis-idaea</i>	0.03
<i>V.myrtillus</i> - <i>Empetrum hermaphroditum</i>	0.05
<i>V.myrtillus</i> - Poaceae	-0.03
<i>V.vitis-idaea</i> - <i>Empetrum hermaphroditum</i>	0.78*
<i>V.vitis-idaea</i> - Poaceae	0.26
<i>Empetrum hermaphroditum</i> - Poaceae	0.05

Table 5.

Occurrence and grazing of four dominating species at three sites. The values are based upon 500 1 m² plots in each site.

I:total percentage occurrence/ percentage grazed

II:mean percentage cover/ percentage grazed cover

I	site b	site i	site m
<i>Vaccinium vitis-idaea</i>	100/72	82/68	100/90
<i>Vaccinium myrtillus</i>	46/82	28/86	84/95
<i>Empetrum hermaphroditum</i>	100/82	88/91	100/94
<i>Betula nana</i>	50/40	94/79	0/-

II	site b	site i	site m
<i>Vaccinium vitis-idaea</i>	8.3/4.3	1.7/1.8	7.8/8.8
<i>Vaccinium myrtillus</i>	3.6/21.0	0.3/8.9	5.9/7.9
<i>Empetrum hermaphroditum</i>	43.5/3.3	25.9/15.9	33.5/3.4
<i>Betula nana</i>	4.2/0.4	19.4/0.4	0/0

Table 6.

Correlations between the frequencies of some species and the proportions of them that were grazed. The figures are based upon results from 15 plots (0.5 x 0.5 m) at site b (cf Fig 1b and text 2.1). $*=p^20.05$

<i>Vaccinium vitis-idaea</i>	-0.31
<i>Vaccinium myrtillus</i>	0.85*
<i>Empetrum hermaphroditum</i>	-0.45
Poaceae	-0.25

Table 7.

Mean number and standard deviation of fresh faeces in different vegetation types during four sampling periods. Plot size, 2.5 dm². For the definition of grazed and ungrazed types, see text.

Ungrazed	Aug 1978	Jul 1979	Aug 1980	Jul 1982
Empetrum type 1978				
(site m)	16+-20 n=5	50+-70 n=3	56+-16 n=2	205+-108 n=3
Grazed				
Empetrum type 1978				
(site m)	3656+-1215 n=5	105+-211 n=3	104+-35 n=2	530+-455 n=3
Grazed				
Empetrum-V.myrtillus				
type 1978	5616+-3324 n=15			

Table 8.

Food preferences of Clethrionomys rufocanus determined from an experiment using caged animals at Abisko in July 1978. Each experiment lasted for 5 hours and 2-4 plant species were fed to the rodents in six combinations. 23 animals were used in the experiments.

The first column presents the mean percentage, and standard deviation, of each plant material eaten in each combination.- The second column presents these values expressed in relation to the most preferred species in the combination.

Combination I:n=10	1.	2.
Vaccinium myrtillus	63 +- 51	100 +- 81
Polytrichum spp.	38 +- 20	60 +- 32
Deschampsia flexuosa	9 +- 3	14 +- 5
Combination II:n=10		
Vaccinium myrtillus	39 +- 12	100 +- 31
Vaccinium uliginosum	21 +- 16	54 +- 41
Empetrum hermaphroditum	7 +- 6	18 +- 15
Vaccinium vitis-idaea	2 +- 4	5 +- 10
Combination III:n=8		
Vaccinium vitis-idaea	73 +- 50	100 +- 68
Linnea borealis	51 +- 25	70 +- 34
Combination IV:n=7		
Empetrum hermaphroditum	28 +- 23	100 +- 82
Linnea borealis	17 +- 23	61 +- 82
Combination V:n=6		
Polytrichum spp.	48 +- 35	100 +- 73
Pleurozium schreberi	36 +- 20	75 +- 42
Hylocomium splendens	1 +- 1	2 +- 2
Sphagnum spp.	0 +- 0	0 +- 0
Combination VI:n=8		
Deschampsia flexuosa	71 +- 11	100 +- 15
Calamagrostis lapponica	28 +- 21	39 +- 30
Festuca ovina	4 +- 4	6 +- 6

II. SHORT-TERM EFFECTS OF TRAMPLING IN SUBALPINE AND ALPINE ECOSYSTEMS IN THE TORNETRÄSK AREA, NORTHERN SWEDEN

SHORT-TERM EFFECTS OF TRAMPLING IN SUBALPINE AND ALPINE ECOSYSTEMS IN THE TORNETRÄSK AREA, NORTHERN SWEDEN.

ABSTRACT

The sensitivity to trampling of a number of sub-alpine and alpine vegetation types was studied using an experimental plot formed like a fan or a circle sector. In this a trampling gradient was produced by walking a number of times from the tip of the sector to the arc of the circle, successively reaching different positions on the arc. The reaction of the different vegetation types was measured after a few months, and after one and two years after the trampling had taken place. Cover, species number, standing crop and diversity were measured.

The ranking scale of the measured vegetation types in respect of vulnerability to trampling was approximately the same no matter what parameter that was used. Fen vegetation was the most sensitive type, withstanding only about 30 passages if its cover two months after trampling was not to fall below 50% of its original value. Thereafter came dwarf-shrub heaths with about 60 passages, and mires with dwarf-shrubs with about 70 passages. Meadow vegetation types could withstand much more trampling, in some cases several hundred passages. Also the meadow vegetation types recovered totally the fastest, in some cases in two years after 1600 passages. Comparing relatively similar vegetation from high altitudes (1200m) with that of low altitudes (350-600 m) it was evident that high altitude vegetation types were not more sensitive than the others, but they recovered slower.

Trampling early or late in the season seemed to affect especially meadow vegetation types less than trampling in the middle of the season. Also, spreading out the trampling on 3-5 occasions had a larger effect than trampling concentrated to only one occasion or spread out on 65 occasions.

1. INTRODUCTION

In 1977 a program was started to study the effects of trampling upon alpine and subalpine vegetation in the Torneträsk area, northern Sweden (Fig. 1).

The aim was both scientific as well as applied: Because of destruction of vegetation caused by an increasing number of hikers in the Swedish mountains, trampling is regarded as a conservational problem needing more research (Liljelund et al. 1977). By means of this program more information should become available for the appropriate management of these areas.

Four projects were included: (1) one dealing mostly with the long-term effects of trampling on vegetation (Emanuelsson 1984a), (2) one with short-term effects (this paper), (3) one with detailed effects of trampling on Empetrum hermaphroditum and some Vaccinium-species, and finally (4), a project dealing with the effects of rodents on some common subalpine and alpine vegetation types in northern Sweden (Emanuelsson 1984b).

The results presented here deal only with the reaction of earlier untouched vegetation exposed to experimental trampling for only a short period, then left protected and subsequently studied.

Associations of plant species resistant to trampling occur in established tracks (Bates 1935, 1938a, 1938b, 1951; Emanuelsson 1984a). These associations are a long-term effect of trampling. Long-term effects and short-term effects should be compared for better understanding of the reaction of the vegetation. The present results and the descriptions of the long-term impact in Emanuelsson (1984a), are therefore complementary when discussing the reaction to trampling in the common vegetation types of the Torneträsk area.

Knowledge of the relative resistance to trampling of different vegetation types and the recovery rate when impact ceases is important for the planning of recreation areas. Thus, work in

the program at Abisko has been allocated to studies of such problems.

During recent decades many investigations have been carried out on the effects of trampling on vegetation. Reviews of the literature have been presented by Liddle (1975a), Satchell & Marren (1976), and Liljelund et al. (1977).

The methods have varied. Some investigators have studied areas already trampled (e.g. Bayfield 1971; Streeter 1971; Dale & Weaver 1974; Karlsson 1974; Falinski 1975;), some have experimentally produced tracks by trampling (e.g. Kellomäki 1973, 1977; Baifield 1979), and some have used equipment especially designed to simulate pedestrians (e.g. Blom 1981).

The aim behind most of these investigations has been to establish the vulnerability of various vegetation types to such influence. In most cases the studies have been made close to or within areas used for recreational purposes.

Since the methods have varied widely, direct comparisons are often difficult to make although some attempts have been made (Liddle 1975b).

Productivity is one general variable proposed by Liddle (1975a) to illustrate the vulnerability to trampling in different types of vegetation.

However, a variable such as the amount of normal grazing in a vegetation type may also be useful.

Since almost all vegetation types are to some extent grazed (Harper 1977), an adaptation by single species to herbivory should take place in nearly all plant communities.

Grazing must at least to some extent also be synonymous with trampling, at least when large vertebrate herbivores are considered.

Therefore the following hypothesis can be formulated: There is a high correlation between the ability to withstand trampling and the intensity of natural grazing in a plant community.

One of the aims of this work was to test this hypothesis.

Comparing investigations of many different trampling regimes in many vegetation types requires an accurate and rapid inves-

tigation method. For this reason the so-called "circle sector method" was developed (Emanuelsson 1978, 1979) allowing a "trampling gradient" to be produced (see 2.2).

The experiments were planned to answer the following questions:

1. Which vegetation types in the northern parts of the Swedish mountains are most and least resistant to trampling?

2. How does trampling affect vegetation in different phenological phases?

3. What is the reaction if the trampling is restricted to only one occasion or spread out over many occasions?

4. What is the correlation in different vegetation types between the ability to withstand trampling and the extent of natural grazing of those vegetation types?

When deciding which biological variables should be used for measuring the changes in the vegetation due to trampling, practical considerations were applied to some extent:

The variables should be easy to observe by eye and quick to measure/estimate in the field at the same time as they should reflect real biological changes in the plant community. Useful variables are, e.g., cover of the plant community, height, number of species, number of flowers, and number of fruits. In the present paper, cover is used to measure the biological status of the plants since it is a rapid method and generally used in studies of vegetation dynamics (Shimwell 1968).

2. METHODS

2.1. The investigation area.

The investigations were carried out in the Torneträsk area (Fig. 1) in the northwesternmost part of Sweden ($68^{\circ}20-30'N$ and $18^{\circ}10-20' E Gr$). The area is characterised by strong climatic gradients and widely varied vegetation. For the purpose of the present investigation it was considered important to compare many different vegetation types.

The mean annual temperature of Abisko, in the centre of the area and at a comparatively low altitude (370 m.a.s.l.), is $-0.5^{\circ}C$ (Sonesson 1980). The precipitation in the region ranges from 300 mm/year at Abisko to about 1000 mm/year in the western part of the region (Sonesson 1967).

The growing period at Abisko is about 100 days/year.

The vegetation covers a gradient in the area from subalpine birch forest (Betula pubescens Ehrh. ssp tortuosa (Ledeb.)Nyman), with Scots pine (Pinus silvestris) in some places, to high alpine tundra.

The geology in the area is complex and, from an ecological point-of-view, both poor and rich soils occur.

The direct human impact of the area has been claimed to be comparatively small (Sonesson 1970, 1979, Sonesson & Lundberg 1974), except "in the immediate vicinity of the railway, the tourist village and tourist tracks" (Sonesson 1979) and the road, running through the area.

For further general information on the ecosystems of the area see Mårtensson (1956), Sandberg (1963), Sonesson (1970, 1979) and Sonesson & Lundberg (1974).

Nomenclature for cryptogams is according to Krok & Almquist (1962), for vascular plants to Lid (1974) and for mammals to van den Brink (1958).

2.2 The investigation plots - the circle sector method.

To save time and to produce a well-defined gradient of trampling, a device shaped as a circle sector was used for the investigations (Fig. 3).

The trampling gradient was produced by repeated walking from the arc of the circle sector to the tip of it, and back again. At each turn the starting point was moved 5 cm along the arc.

The length of the arc was 5 m, meaning that the position of the starting point changed 100 times before the investigation plot was fully trampled. The radius of the circle sector was 5 m to give a certain relationship between the distance from the arc to any point on a line between the tip and the arc, and the trampling intensity at that point.

Different points can be compared in these investigation plots since the relative trampling impact will be well defined, provided the same person is involved in the work.

To get comparable results for different circle sectors trampled by different persons, the following formula was used to give the number of standard passages (by a person weighing 70 kg with a length of step measuring 0.7 m) at any point in the circle sector:

$$\frac{A \times B}{5 \times D \times C} = \text{number of passages by a 70 kg person with a 0.7 m step.}$$

A = number of times which the circle sector will be fully trampled

B = weight of the person (kg)

C = length of a step of the person (m)

D = distance from the tip of the circle sector to a certain point for which the amount of trampling should be calculated.

Since the opening at the tip of the investigation plot is 20 cm (also approximately the width of the "corridor" that the experimental persons used when walking straight forwards on horizontal ground) and the arc of the plot is 5 m, the trampling intensity at the arc will be 25 times less than at the tip of the plot. To increase the range of trampling intensities a second investigation plot in the same vegetation on the same occasion was sometimes added. When, for instance, a second plot was trampled 20 times more than the first one, the total amplitude obtained was 1 to 500 trampling passages instead of 1 to 25.

For comparison of the investigation plots with untrampled vegetation and to check at the same time that no other environmental gradient coincidentally ran in the same direction as the trampling gradient, two non-trampled zones (50 cm wide) were delimited immediately outside the trampled plot and investigated in a similar way.

2.3 The investigated vegetation types.

There were two different criteria for the selection of vegetation for use in the present investigation: (1) the type should be common in the area; (2) the investigation should cover a wide range of different vegetation types.

Within the common vegetation types there was a selection of plots according to wetness, nutrient conditions, altitude and grazing regime, although plots satisfactorily covering all gradients could not be found.

Emphasis was placed on the nutrient and grazing pressure gradients.

In order to have some extreme vegetation types along the altitudinal gradient, four plots were selected in the middle alpine belt above the so-called podsolation limit (Sjörs 1956). One of these types was a sedge and grass dominated type (plots 27,28), the other type was dominated by dwarf-shrubs (plots 29,30).

All other chosen vegetation types were situated in the low alpine or in the subalpine belts.

The range in altitude of these plots in the low alpine and subalpine belts were not more than 200 metres in altitude so it can be assumed that altitude was of little importance for the differentiation of the vegetation. The altitudinal influence discussed here is based on the comparison between these four plots in the middle alpine belt and the other plots in the low alpine/subalpine belts.

2.4 The investigation of the circle sectors after trampling.

The study of the circle sectors was performed by a sub-sampling technique: A device similar to a rope-ladder was constructed; 0.1 m broad and 5 m long, divided into 50 squares, each measuring 1 dm².

The rope-ladder was placed in seven positions with one end at the tip of the circle sector and the other end in seven different positions at regular intervals along the arc (Fig 2). Each of the 50 squares so formed by the rope-ladder was randomly numbered between 1 and 7.

These numbers corresponded to the seven positions in which the rope-ladder was placed. A square was only considered when the ladder was placed in a position corresponding to the random number (1-7) of the square. By means of this system, fifty 1 dm² squares were investigated in each circle sector. In the two non-trampled zones every sixth square was investigated. In all squares the cover of the species in percent was estimated. In the squares trampled only in July (see Table 3), soil samples as well as samples of the biomass were taken the same year in the middle of September using a peat sampler measuring 2.5 dm². Five such samples were also taken in the non-trampled reference zones of the circle sectors trampled in July.

2.5 Time schedule of the investigations (see Table 2a and b.)

Most of the experiments were done in 1978. One pilot circle sector was trampled already in 1977, and in another the trampling was spread out over the whole growing period of 1979.

Finally, four circle sectors situated in the middle alpine zone were trampled in 1979.

Circle sectors treated only on one occasion were either trampled in the middle of June, July, or in August. Those treated three times were exposed on one occasion in June, July and August respectively. Those treated five times were also trampled on one occasion on July 1 and again on August 1 (see Table 1b.).

Sectors trampled five or three times were exposed to exactly the same total "amount" of trampling as those exposed on only one occasion.

Possible seasonal differences in the ability to withstand trampling were studied by treating plots of the same vegetation type on different occasions during the year.

By concentrating the trampling to only one occasion in some plots and spreading it over three, five or many occasions (one treatment involved trampling every day for 64 days during the summer), any differences in response could also be studied.

The analyses of frequency, cover, etc., of the vegetation were always carried out by late August or early September. Soil sampling as well as biomass measurements were performed only in early September 1978.

2.6 Statistical treatment.

A. The composition of the vegetation investigated is shown in Table 2a and b, where each species in each circle sector is represented by two figures. One figure gives the mean cover in the reference zones and the other the frequency of occurrence in the sub-samples in the reference zones.

B. The cover of the species was the parameter used most for describing the changes that took place in the vegetation due to trampling.

Both the total cover of all species as well as cover of single species were measured.

The cover was related to the amount of trampling by the following procedure:

For each square in the circle sector the amount of trampling to which it had been exposed was calculated. See 2.2.

For each square of the circle sector calculations were also made of the relative cover compared to the mean cover of the squares in the reference zones.

These cover values and the amount of trampling were then plotted, and three types of curves were fitted; viz. calculated linear and logarithmical curves and curves fitted to the data by hand (Fig.4).

To be able to compare the results of the regression analyses (Sokal & Rohlf 1969) with each other a table was constructed (Table 4) to show the amount of trampling within 95% confidence intervals which is needed to reduce the normal cover (i.e. cover in reference zones) by 50% .

From the curves it is also possible to find a certain cover value which will result after 200 passages (Table 5).

Finally, in some cases it is possible to predict from the diagrams the number of passages that a vegetation type can withstand and still totally regenerate in three years (Table 6).

The number of passages necessary to reduce single species to 50% of their original cover values is shown in Table 10.

C. The numbers of species in relationship to the mean number of species in the reference zones were plotted against the amount of trampling (examples in Fig 6, summarized results in Table 7-9).

D. The change in cover along the trampling gradient for each species in a circle sector was compared to the total change in cover for all species lumped together. From this can be deduced whether a certain species increased or decreased in relationship to others as trampling was increased (Table 11)

This was performed using the data of most circle sectors in 1978.

Most species showed no statistically significant results (95% confidence limit), although some species showed a marked negative or positive tendency. In Table 11 this is marked by + or

- signs. Results falling between the 85 % and 95 % confidence limits are shown by (+) or (-).

Species that had only very few occurrences in the circle sectors are not marked, but those with occurrences in more than half of the squares in the reference zones are marked with 0 if their confidence values are not higher than 85 % (Table 11).

E. To show the short-term change in biomass, ten samples were selected in the trampled part of a number of circle sectors in September 1978 and five samples were also taken from the reference zones of those circle sectors (Fig. 2).

The same method was used to decide where the samples should be collected so as to decide which squares should be investigated with regard to cover (Fig. 2).

The relative biomass (amount of biomass in relation to the mean biomass in the reference zones) was plotted against the amount of trampling (Fig. 9). In this context, biomass means live above-ground tissue (dryweight).

F. Diversity indices were calculated for the cover of subsamples selected in the circle sectors and in the 17 subsamples taken in the reference zones.

Simpsons index (Simpson 1949) was used:

$$D = 1 - \sum_{i=1}^S \frac{n_i(n_i-1)}{N(N-1)}$$

where S stands for the total number of species in the subsamples, N for the total cover of the sub-sample and n_i for the cover given by the i :th species.

G. Correlations between grazing pressure and ability to withstand trampling are shown in Fig. 11. Data on the ability to withstand trampling were taken from Table 4 (representing July).

Figures on grazing could not be obtained, however, and thus indirect information was used, i.e., the number of small rodent droppings found in the biomass samples of the reference zones. The reindeer grazing figures are only estimates of the numbers of grazing reindeers on 5 occasions from June 1 to Sept. 15, 1978.

3.RESULTS

3.1. Changes in cover (Figs 5a-d and Tables 4-6)

In most cases the cover values of the trampled vegetation was decreased for a period after the trampling took place. After a minimum cover was reached recovery took place, but the whole process varied very much in time.

The reaction of the vegetation to trampling was by no means linear to the amount of trampling and instead was often logarithmical.

The cover increased in all parts of the trampled circle sector as time passed (Fig. 5a).

Most of the 30 circle sectors showed this tendency but exceptions were some circle sectors placed in Dryas-vegetation, low-herb meadow and tall-herb meadow.

The most intensively trampled areas of the circle sector recovered faster than the moderately trampled parts (Fig. 5b).

Vegetation types dominated by a few species, such as the Empetrum-heath (Fig. 5c) and mire-vegetation, showed a more regular pattern in recovery than vegetation types richer in species (Fig. 5d). The latter types also show more linear curves compared to the "few-species"-types (Fig.5c).

Using this type of diagram for a simple ranking of the different vegetation types according to their ability to withstand trampling is difficult. As can be seen from the curves, one vegetation type may withstand trampling better than another at one intensity of trampling, while in another range of trampling intensity other vegetation type may be the most resistant.

Many ways of summing up, but thereby generalizing, the results of such diagrams described above can be done. Two ways are used in Tables 4 and 5 (see 2.6.2).

In all cases the fen vegetation was the easiest to destroy by trampling, although the Empetrum-heath was also especially susceptible in this respect (Tables 4 and 5).

In the ombrotrophic peat bog dominated by Empetrum hermaphroditum, trampling also gave clear results even after relatively few passages, but it is worth noting that this vegetation type withstands trampling better than the very similar Empetrum-heath which was growing on mineral soil.

The heath vegetation dominated by Vaccinium myrtillus also showed a reaction to trampling very similar to the Empetrum-heath.

The three types of meadow-vegetation that were tested in this investigation (low-herb meadow, tall-herb meadow and herb-fern meadow) all showed an overall better resistance to trampling than the heath vegetation types, the low-herb meadow being the best.

The meadow vegetation types were also much better than the heath types in rate of recovery.

The grass-heath types and dwarf-shrub types of the middle alpine belt both showed a relatively good ability to withstand trampling, although their recovery rates were low.

For some vegetation types, e.g., the low-herb meadow, it was found that the time of the season when the trampling took place was of great importance for the reaction of the vegetation. When this vegetation type was trampled in the middle of the growing season its negative response was greater than if trampled early in the season. The same result, although not so clear, was obtained in the tall-herb meadow.

There was also a weak tendency in many vegetation types to react more when the trampling was spread out over many occasions than when concentrated to only one (Table 4).

The present paper also gives figures for the amount of trampling a vegetation type can withstand if it is to recover after a certain time. This is shown in Table 6, in this case giving the maximum number of passages a vegetation type can be exposed to if recovery is to be total after 3 years. Few vegetation types were capable of such recovery if the trampling was more than approximately 100 passages.

3.2 Changes in numbers of species (Tables 7-9).

Correlations are made in the present paper between amount of trampling and the number of species in the trampled areas. These correlations indicate that there is often a linear relationship between the natural logarithm ($\ln$) of the amount of trampling and the number of species (Fig. 6a).

In most vegetation types the recovery of the number of species was quite regular in parts of the circle sectors that had been moderately trampled (see e.g. Fig. 6b). In the more heavily trampled parts of the circle sectors the recovery pattern of the number of species was more complicated. Here the number of species, especially after three years, could be higher than in the parts of the circle sectors which had been exposed to less trampling (Fig. 6c).

The curves in the diagrams which represent the numbers of species in three different years are frequently not parallel. Instead, a majority of them are diverging, showing that the differences in number of species between the years were greatest in the most trampled parts of the circle sectors (Fig. 6b,c and d).

The extent of trampling that the vegetation types could withstand without losing more than 50% of their species (Table 7) was usually quite high. Even if the vegetation types were treated by as many as 1600 passages (fen trampled in mid July, Empetrum-heath trampled 3 and 5 times during the season), only a few circle sectors (combinations of vegetation types and treatments) still contained less than 50% of their original numbers of species after three years.

The fen vegetation type lost most of the species after trampling (Tables 7 and 8). The meadow vegetation types resisted trampling best judging from the number of species. Other vegetation types were intermediate. No trends towards different reactions in the number of species relative to different times of trampling during the season were observed (Tables 7 and 8). One vegetation type that showed a very different reaction compared to the other types was the Dryas-heath. This vegeta-

tion type (Fig. 6e) lost about 35% of its species stock whether trampled 1600 or only 64 times. Recovery in number of species was also very poor.

A complete set of data showing total recovery in number of species after 3 years could not be obtained for practical reasons. However, Table 9 gives figures for vegetation types from which data were obtained. In many cases the meadow vegetation recovered totally after 3 years even with a trampling pressure of 1600 passages (Table 9). Other types could only resist a few hundred passages to be able to recover totally. The fen vegetation was the most sensitive.

3.3 Changes in diversity (Figs. 7 and 8).

The diversity in low-herb meadow types was only little affected by trampling. After half a season no differences in diversity were detected between heavily trampled and untrampled areas (Fig. 7). In contrast, the tall-herb meadow type responded more. Even slight trampling resulted in significant lowering of the diversity and additional trampling had little effect only (Fig 7). The diversities of the wet ecosystems (fen and mire) were more affected by trampling than the meadow types (Fig. 7). Their reactions were also better correlated to increased trampling compared with the reactions of the meadow types.

The reaction of the heath vegetation types was more complicated (Fig. 8c). The diversity was first depressed by light trampling. Medium trampling resulted in a raised diversity, while even more trampling resulted in a low diversity.

In most vegetation types the diversity rose considerably in the most trampled parts of the circle sectors after one or two years.

3.4 Standing crop.

Marked changes in standing crop later in the season of the same year that the trampling took place were recorded for most of the vegetation types tested. The standing crop of especially the fen vegetation was severely reduced by trampling, but also that of vegetation types such as the tall-herb meadow (Fig. 9).

In terms of standing crop, the low-herb meadow and the Dryas-heath were resistant to trampling. The standing crop of the Dryas-heath differed only little between the lightly trampled parts and the heavily trampled parts of the circle sector.

The other vegetation types were intermediate in terms of resistance to trampling in the same year the treatment took place.

The low-herb meadow totally recovered in terms of standing crop 2 years after 1600 passages while after 2 years with the same amount of trampling the Empetrum-heath carried still only 50% of its original standing crop (Fig. 10a and b).

3.5 The tolerance of some species to trampling (Table 10).

All the species in the fen were able to withstand less than or approximately 30 passages before they were decreasing to approximately 50% of their original values.

Species commonly found in heath vegetation types such as Empetrum hermaphroditum, Vaccinium vitis-idaea and Vaccinium uliginosum decreased already at a relatively moderate trampling impact.

Vaccinium myrtillus resisted trampling better than the other dwarf-shrubs.

Three grasses, Anthoxanthum odoratum, Roegneria borealis and Deschampsia flexuosa resisted approximately 120 passages before their cover decreased below 50% of the original values.

The figures for herbs were of the same order as for the grasses, although with higher variations.

Some herbs, i.a. Rubus saxatile and Gnaphalium norvegica, increased in cover although this change was not statistically significant.

Among the mosses studied it was obvious that the species growing in fens were more sensitive than, for example, Pleurozium schreberii typical in terrestrial sites. Sphagnum species were the most susceptible plants studied in the present investigation.

Many species depended highly upon the type of soil and the vegetation type in which they grew. In other words, the same species withstood trampling very well in one vegetation type, while in another vegetation type it suffered severely from trampling.

The most extreme example of this phenomenon was Andromeda polifolia, which tolerated 105 passages in an ombrotrophic mire but just 20 passages in a wet fen before more than 50% of its cover disappeared. Other species showing a significant difference in ability to withstand trampling depending on soil and vegetation type were Empetrum hermaphroditum, Vaccinium uliginosum and Rubus chamaemorus.

Finally, it should be mentioned that many species present in the vegetation types investigated were so sparse that it was not possible to estimate how much trampling they could tolerate.

3.6 Relative changes of importance of some species after trampling (Table 11).

The relative importance of a species may increase in a trampled vegetation type even if the absolute cover of the species is lowered by the trampling impact.

The relative reactions of the more common species in the circle sectors are given in Table 11. The table shows whether one

species is getting more or less abundant in relation to the other species in a vegetation type. The figures are from early September in the same year as the circle sectors were trampled. Changes in the following years were few but the following species were found to increase in cover, relatively, during the first year: Alchemilla sp, Polygonum viviparum, Arcostaphylos alpina, Veronica fruticans, Viola biflora and Andromeda polifolia.

Some species which did not gain the first year from trampling but later were: Vaccinium vitis-idaea and Rumex acetosa. Vaccinium myrtillus became relatively more abundant in heath-vegetation types but became relatively less important in nutrient-richer vegetation types as a result of trampling.

Already in the first year Sphagnum-species, Empetrum hermaphroditum, Trollius europaeus, Carex capillaris and Dryas octopetala became relatively less abundant due to trampling. This tendency was increased during the second and third years.

3.7 Relationship between natural grazing regime and ability of a vegetation type to withstand trampling.

There was a clear relationship between numbers of small-rodent droppings and the resistance to trampling in the vegetation types tested (Fig. 11).

Since the occurrence of reindeers was only roughly measured it can only be stated that there was some relationship between the occurrence of reindeers in summer and resistance to trampling of the vegetation.

4. DISCUSSION

4.1. The representativity of the results.

Eleven different vegetation types were investigated representing the most common vegetation types in the Torneträsk area. (See the vegetation map of the Torneträsk area; Vegetationskartor 1979-84).

It should therefore be possible to transform the results of the present investigation to a map showing the susceptibility of certain areas to trampling. For some intermediate vegetation types which were not investigated it is probably justified to estimate their resistance to trampling by interpolation using results from the present paper. Such estimations are likely to be fairly reliable judging from the results from the trampling studies in vegetation intermediate to other types tested. Thus, for example, the meadow-like vegetation type dominated by Vaccinium myrtillus was intermediate to the low-herb meadow and the Empetrum-heath in resistance to trampling.

Looking at the whole mountain area of northern Sweden this investigation can hardly be regarded as complete as for example, no typical Cladonia-dominated vegetation types were investigated.

However, if we consider a mountain area above the tree-line in the province of Jämtland approximately 80% of the surface there can be classified according to its vulnerability to trampling using the results of the present investigation.

It is probable that many of the mountain areas above the tree-line in Sweden can be roughly classified as regards trampling vulnerability with the aid of the present investigation together with vegetational maps (Vegetationskartor 1978-84) which have been recently produced.

4.2 The method.

The method presented, i.e. "The Circle Sector Method", is certainly time-saving compared with, e.g., the method of using

experimental tracks (Satchell 1976, Liljelund et al. 1977). Another advantage of the method is that it allows studies to be made of the continuous trampling gradients necessary for an accurate estimate of the reaction of vegetation to a given trampling intensity.

Using the circle sector method also allows us to simulate and quantitatively study diffuse trampling. However, it may thus also be difficult to directly relate these results to the results of mere trampling on a track. Tracks for example, will also canalize water, thereby leading to other effects on both vegetation and soil (Bates 1935; Bryan 1977). By using the circle sectors the effects of trampling can be studied from a more general point of view, i.e., studies of the primary reactions of vegetation to trampling. In tracks, several secondary phenomena affecting the vegetation have to be considered. This means that all results from the circle sector method cannot with certainty apply to the common tracks, and especially not to the older, well established ones.

What the results do show, however, are some major phases in the process of "track formation".

In many sectors investigated, fairly low cover values were obtained in the least trampled parts, whereas more intensively trampled areas showed higher cover values. This phenomenon was probably an experimental error caused by the individual doing the trampling, when an unnaturally pronounced step was taken when entering the circle sector. This error can be avoided if the least trampled parts of the circle sectors are excluded from the analysis, as was done in some obvious cases in the present study.

For studies of the immediate reaction to trampling the circle sector method seems to be ideal, although less useful in studies of the recovery of vegetation trampled earlier. The shape of the circle sector is a particular disadvantage in this case. At the tip of the sector, which will be the most trampled part, the distance to untouched vegetation will be, on average, much shorter than at the arc. Thus, the parts trampled most heavily are also those where revegetation by colonisation of vegetatively growing clonal plants will have the best opportunities.

A modification to improve the method may be to place a mechanical barrier, e.g., a metal plate, in the soil to delimit the reference zones and to stop vegetative recolonisation.

The type of diagram presented, for example, in Figs 4 and 5 shows the reaction of trampled vegetation to wide a range of trampling impacts. To be able to compare numerous such diagrams, specific points in them were selected and presented in Tables 4 and 5.

However, one should remember that such a comparison may give only a limited view of how vegetation reacts to trampling since this shows only the reaction at certain trampling levels. This becomes obvious when Figs. 6e and f are compared.

Four different ways of selecting points for comparison have been used and are presented in Tables 4 and 5. These tables contain a vast amount of information but it may be difficult to use them to obtain a general impression of the order of trampling resistance in the vegetation investigated.

Therefore, in Table 12, only results of circle sectors trampled on one occasion in mid July are presented.

4.3 Choice of investigation plots in the field.

Instead of placing, for example five circle sectors in each experimental set-up, i.e. altogether 145 experimental sectors, only one was investigated in each of the 29 combinations of vegetation types and treatments. This was done both for practical reasons because of limited time and since the procedure would be sound from statistical and biological points of view. Since 50 subsamples from which the individual trampling pressures could be obtained were taken along the trampling gradient of a circle sector, it was possible to calculate the confidence intervals of the regressions between trampling pressure and the variables of the vegetation. In other words, it was possible to get a figure for the uncertainty of a value calculated from a single circle sector experiment.

This, of course, means that figures found in an experiment dealing with a particular circle sector will only with cer-

tainty represent the conditions in that particular circle sector.

However, the results should be representative of a much larger area since they all fit well into a pattern from which it is possible to predict the reaction of trampling in intermediate vegetation types. Thus, for example, V.myrtillus vegetation has been discussed above in this context. Also figures for the fern-herb-meadow, which floristically is an intermediate form between the tall-herb meadow and the low-herb meadow, confirms this (compare Tables 2 and 4).

4.4 Comparison of parameters used in the present investigation.

Different parameters used to describe what is happening in the vegetation if an area is trampled will give very different general impressions.

From a planners point of view, cover is often a relevant parameter since usually the only information required is whether the soil under a certain trampling regime will still remain covered with vegetation. In many such situations the vegetation will change from a type sensitive to trampling to a more resistant type. The cover will then not be changed but the species composition will.

In the present investigation, where most of the trampling took place in just one growing season, a marked decline in cover was recorded for most of the vegetation types if trampling exceeded 200 passages. However, there was no large decline in number of species in any vegetation type and, even more important, almost no new species invaded the trampled areas during the three years of the experiment.

This indicates that the investigated vegetation types need a more permanent type of trampling regime to be converted to new vegetation types resistant to trampling.

Emanuelsson (1984a) demonstrated what such "converted" vegetation types can look like. They can be studied along tracks moderately used over long periods.

4.5 Cover.

Generally it is hard to compare the results obtained in the present investigation with other already published results, as the methods have been shifting from investigation to investigation. However, in the present investigation the same method has been used when studying a number of vegetation types. Therefore most of the discussion dealing with comparisons between different vegetation types is carried out without mentioning detailed results obtained by other authors.

It can be mentioned, however, that corresponding studies by Kellomäki (1973, 1977) and by Bayfield (1979) generally arrived at similar results. Karlsson (1974) stresses much that wet vegetation types are generally more sensitive than drier ones. Also Liddle (1975a) and Satchell & Marren (1976) points to the fact that the wetness is important for the sensitivity of the vegetation types.

In the present study the cover in nearly all vegetation types decreased during the first weeks after the trampling had taken place. This initial decrease was only documented by colour photos. At least in the more trampled part a decline in cover was recorded already at the first investigation in September of the same year.

In some cases the response was extended, for example in the Empetrum-heath, where the decline proceeded for two years after the trampling had ceased. A similar result was obtained by Bayfield (1979) with Empetrum nigrum and Calluna vulgaris.

Apart from the Empetrum-heath all the vegetation types began to recover after slightly more than one year.

Some unexpected results on the recovery in the low-herb meadow were obtained; in severely trampled vegetation the recovery was faster than in medium trampled parts. This was probably a result of a colonisation, possibly in combination with a favourable nutrient situation.

The trampled fen vegetation was the type that had the lowest cover values if compared with untrampled similar vegetation.

This is seen in all types of diagrams. The explanation of this high sensitivity must be that the peat soil of this vegetation type is wet and soft and that a walker will easily sink into the soil and also twist it, thus particularly damaging the moss layer.

Second to the fen vegetation in terms of vulnerability to trampling comes two types of heath vegetation; Empetrum-dominated heath and Empetrum-Vaccinium myrtillus-dominated heath. The Empetrum-dominated type seems to be the most vulnerable of the two types, at least at an initial stage after trampling. The recovery will be faster in later stages in the Empetrum-dominated vegetation, however.

This result does not agree with other observations on the relation between Vaccinium myrtillus and Empetrum hermaphroditum (Emanuelsson 1978, 1984a). In these investigations Vaccinium myrtillus was found to recover faster than Empetrum hermaphroditum. However, one should remember that in the above mentioned comparison, entire vegetation types are considered while Emanuelsson (op. cit.) deals only with single species.

Some ombrotrophic mires in the area are also characterized by Empetrum hermaphroditum. The site used for the present investigation was drier than most similar ones in the region, and perhaps because of this it could withstand trampling fairly well.

Ombrotrophic mire vegetation resisted trampling better than vegetation in the heaths of a similar floristic composition. One explanation of this may be that the peat is elastic and will sag when trampled, whereby the plants will not be crushed as in similar situations in terrestrial sites on mineral ground.

However, trampling starts soil erosion on peat soils more easily than on mineral soils (Bryan 1977), although these effects will be apparent only at trampling levels that are much higher than those used in the present investigation.

The results of this material show that mire and heath vegetation types are more vulnerable to trampling than vegetation

under better nutrient conditions, i.e. the meadow types (cf. Sjörs 1956).

There are exceptions from this general pattern: the dwarf-shrub vegetation of the middle-alpine belt (1200 m above sea level) which is fairly resistant to trampling, is more resistant than dwarf-shrub heaths of the low-alpine and sub-alpine belts.

However the regeneration after trampling is slow in this vegetation.

Probably the good resistance to trampling of the middle-alpine dwarf-shrub heaths can partly be explained by the extreme growth form of the dwarf-shrubs, here very seldom growing more than 5-8 cm above the ground. Trampling will not break the lignified shoots of these low forms as it will do in more prostrate forms in the low-alpine belt.

The middle-alpine dwarf-shrub heaths are also richer in species than the low-alpine ones, and the sensitive Empetrum hermaphroditum is not as dominant.

The meadow types generally regenerate well, especially the tall-herb meadow. On the other hand, in the very short run these tall-herb meadows will be changed a lot by trampling, which may explain the common view that this type is vulnerable.

The good recovery of the meadows can be explained by the ability of the plants in these vegetation types to regenerate from subterranean parts. Especially if the trampling impact is concentrated to only one growing season there are probably good opportunities for the meadow-plants to recover rapidly. However, continuous trampling for several years, even light trampling, will probably give relatively equal results in both meadow and heath vegetation.

Information on how much trampling a vegetation type can withstand if total recovery is required after a certain number of years, has an obvious applied interest, e.g. for planning purposes.

The present material permits such information to be obtained for a three-year period:

The fen vegetation is the most sensitive also in this respect.

Only around 30 passages were possible if this vegetation type was to regenerate totally after 3 years. However, most of the other vegetation types seem to withstand around 200 passages to regenerate totally after 3 years.

Even if the meadow vegetation seems to regenerate a little better than the heath-types it is surprising how equal they are in terms of total recovery.

Some vegetation types react very differently to trampling depending on the time of the year when the trampling takes place.

Both tall-herb and low-herb meadow vegetation are more resistant if the trampling takes place in June than in July or August.

A possible explanation of this phenomenon may be that the herbs in June have only translocated a minor part of their stored assimilates and nutrients to the above-ground tissues and therefore still have a relatively large reserve to be used if above-ground tissues are damaged. In July and August these reserves are smaller or depleted.

However, regarding the heath and mire vegetation types, no such seasonal differences can be traced. Probably there are much smaller amounts of translocates involved in seasonal transportation cycles in the heath than in the meadow vegetation. Much more assimilates are stored in the above-ground parts of dwarf shrubs than in herbs, in which nearly no assimilates are stored above-ground.

Thus, at all times of the year trampling will influence the dwarf-shrubs in roughly the same way, but this does not apply to many geophytes of the meadow.

Trampling concentrated to only one occasion or distributed over several occasions can give different results.

If the trampling is distributed over three or five occasions a slight tendency for an increased effect can be traced at least during the first year after trampling in the Empetrum heath.

However, it is doubtful whether there is a real difference in result between areas trampled on only on one or on three or five occasions. This may possibly be just an effect of part of the trampling being done late in the season when some vegeta-

tion types may be more influenced than if they were trampled earlier.

The more pronounced reaction of some vegetation types after being trampled on several occasions seems to disappear after one year.

On the other hand, it is worth noting that when the trampling was spread out over 64 occasions, in the Empetrum-heaths, the effect did not seem to be as large as when the trampling was concentrated to one, three or five occasions. The effect seems to be much smaller, especially after one year.

4.6 Number of species.

From the results of all circle sectors in the present investigation it is obvious that the numbers of species are diminishing at a much slower rate than the total cover of the vegetation.

In fact, these two parameters change quite regularly in two different ways according to trampling. The curve representing cover falls off much faster than the curve representing the number of species.

Since the nature of the trampling implies that the trampers feet will be placed randomly, some small spots may be trampled to a smaller extent than the rest of the sector, thus causing "lightly trampled islands" in areas more heavily trampled. This will allow many species to survive, although in low abundance and certainly explains the small decrease obtained in number of species.

When cover is considered as a whole, such "islands" are of little importance.

Both the relationships between cover and initial trampling and between number of species and initial trampling will continue to follow principally the same type of curves during the two years following the trampling. The principal differences between "cover curves" and "number of species curves" will remain, even if the positions of the curves will change.

Only few new species, if any, will immigrate into the trampled circle sectors. Seedlings were found only in the meadow vegetation types, although also here infrequently. These observations indicate that the recolonisation takes place by vegetative growth.

Judging from the speed with which many herbs recolonize even severely trampled parts of meadow vegetation, it seems probable that many herbs can survive as subterranean parts alone for at least one year.

One drawback with the circle sector method, as already mentioned, is that vegetative regeneration from outside can take place more easily at the tip of the sector than in less trampled parts at the arc. This might have increased the number of species in the most trampled parts of the plot in a way that was not measurable. This factor may perhaps play an important role in shaping the "number of species diagrams". Perhaps the number of species in trampled circle sectors could be still less if the possibility of vegetative growth from outside was prevented.

In general, all species have re-appeared in the trampled plots after three years. The only exception was in the fen, where the regeneration must be very slow.

The same order was recorded between the vegetation types with regard to the response to trampling. This was shown both in the number of species and in the cover. The reason for this is unclear.

The Dryas vegetation reacts very differently to other vegetation types with respect to the number of species. The magnitude of trampling is of little importance for how many species will be left in the Dryas vegetation. Regeneration also seems to be very poor in the Dryas vegetation if the number of species is taken as an indication of this. This result is strange and has no parallels in the rest of the material. It is difficult to find more convincing explanations. No species in the Dryas vegetation showed a significant trend of becoming relatively less important due to trampling (Table 12).

However, since many species are rare their relative reaction could not be measured. They are easy to exterminate even if they are not more sensitive than Dryas octopetala.

One of the general results of this investigation was that the number of species does not significantly increase over the initial number of species present before trampling. Mainly two conditions may explain the number of species remains low even after, for example, three years of regeneration. Firstly, the vegetation is dominated by species which reproduce vegetatively. Secondly trampling will compact the soil and therefore create overall less favourable soil conditions. In many other cases of soil and vegetation disturbance, for example due to grazing, the soil will be broken up which may improve possibilities for seed germination and invasion of rhizomes, etc.

4.7 Diversity.

Many different ways of expressing diversity have been used. No real agreement has been reached between the authors about which formula should be used.

Two constituents are integrated in the diversity formulas: the number of species and how evenly these species occur. Many species which occur in equal amounts give high diversity. The problem is that different formulas stress the number of species and the evenness to different degrees.

The formula used here, Simpson's method, stresses the evenness to a moderate degree. So for example if the dominance of one common but vulnerable species (Empetrum hermaphroditum) will be broken by trampling this will result in a marked rise in diversity in the vegetation.

In the more intensively trampled parts of circle sectors with Empetrum-dominated vegetation the diversity will be quite low as a result of extensive exclusion of species. The low diversity will here remain for some years. However, in parts of Empetrum-plots trampled most the diversity will rise considerably after only some years, probably as a result of colonisation. It seems possible that this type of colonization can only be effective if the trampling has been so intensive that

the mineral soil is exposed. Those parts that were very slowly colonized still had a peaty layer left after trampling.

In mire vegetation with some Empetrum hermaphroditum an overall lowering of diversity was found in the most trampled areas after one year. A similar colonisation as in the Empetrum heath was found here. The increase in diversity in the Empetrum heath which is not found in the mire, can be explained in terms of dominance of Empetrum. In the mire Empetrum is much less dominant, and a destruction of the species here does not result in such great changes in proportions between species as in the heath vegetation.

Meadow-types found in the Torneträsk area are all relatively diverse compared to the heath-types and usually have larger numbers of species.

The grazing, which is an important ecological factor in the meadow vegetation, probably promotes a high diversity whereas trampling seems to lower it, although the effects remain only for a short period. This is probably a result of the adaptation in those vegetation types to mechanical impact from grazing animals.

4.8 Biomass.

Biomass as a parameter for measuring the impact trampling may to some extent be misleading since biomass is not the same as production. One can assume, for example, that trampling excludes some ericaceous species with a relatively large biomass, increasing the abundance of grasses with a lower standing crop, although with a higher production and rate of turnover. In such a case, biomass measurements carried out only once a year do not give us much information about the actual production.

No measurements were made of the production in the present investigation. However, if only assuming a significantly higher proportion of annual production in relation to biomass in the meadow vegetation than in the heath vegetation, which cer-

tainly is a modest assumption, this may to some extent help us to get a picture of the production in relation to trampling. At least for the meadow vegetation types, biomass and production can be compared to some extent.

Difficulties in measuring production may explain why trampling never caused an increase in biomass or production above the level that prevailed prior to trampling. Rises in production have been found by other authors in trampling experiments (for example Kardell 1980) and also in investigations where experimental grazing was performed (Harper 1977).

Two factors may be of importance here as the biomass was fairly low in the present investigation compared to other similar investigations. Only a few measurements were made three years after trampling, and it is probably not until after such a timespan that high biomass values can be found. The other reason should be that in many trampling experiments the trampling was so intense that the soil was turned around, and mixing with nutrient-rich soil took place. Except for the fen, such mixing did not occur in the present investigation.

4.9 Response of some species.

Two conditions are especially important for the ability of plants to become dominant in newly trampled areas.

Firstly the species should be able to withstand mechanical impact, and secondly, the species must be able to grow rapidly during the seasons following the trampling.

Herbs and grasses are the least vulnerable groups (Table 4). Among the grasses, Festuca sp. seems to resist trampling best although the results obtained were not quite statistically significant (Table 4).

Resistant herbs are Alchemilla spp. and Potentilla crantzii. Although the figure for Potentilla crantzii was not significant due to low abundance, this species is probably also resistant. Both species grow close to the ground and do not expose their apical buds.

In general, plants with woody stems, e.g. Vaccinium spp. and

Empetrum hermaphroditum, seem to be more sensitive to trampling than herbs and grasses (Table 4). The ligneous stems will probably be easily broken and trampling on a single occasion may destroy parts that have developed over several years, while herbs and grasses mostly lose parts developed only during one year.

As regards the lichens, it seems probable that differences in water content in the thalli when the trampling takes place have been of great importance for their ability to withstand the impact. Some differences in weather conditions occurred at the different trampling occasions and perhaps this was enough to cause the great differences in trampling resistance that occurred between different trampling occasions but within the same species.

In general, mosses are vulnerable but a great variability is found among them. Those growing under wet conditions seem more sensitive than those growing under drier conditions even looking at the same species.

A similar trend was also observed among phanerogams, for example, in Andromeda polifolia. Many such examples can be found.

Often such differences in resistance are due to the site of the plant. Such variation within one species may often be greater than between most species in a given environment.

A general conclusion may therefore be that the sites are of greater importance for the ability of a species to withstand trampling than its general adaptation, i.e. genotype.

4.10 Factors important for determining the vulnerability of vegetation types due to trampling.

Summarizing the different results in this investigation, one may ask what characteristics make a vegetation type vulnerable or resistant to trampling.

The answer is not simple since the response to trampling involves many reactions, e.g. changes in number of species,

biomass or cover. Time must also be considered, i.e. whether trampling occurred only on one or on several occasions. Thus, one vegetation type may be regarded as simultaneously being both vulnerable and resistant to trampling depending upon the parameters measured and the time involved.

In the present investigation, correlations between the resistance or vulnerability to trampling in the tested vegetation types and other biotic and abiotic factors, such as altitude, biomass and soil wetness, were poor.

The number of droppings from small rodents as a measure of herbivory, however, was positively correlated with the sensitivity to trampling of the vegetation types investigated. Also the reindeer grazing showed a slight correlation with the resistance to trampling.

However, it may be doubted whether this correlation (Fig. 11) is reliable since it describes trampling resistance in an arbitrary manner. However, similar results are obtained if resistance values from Tables 4, 5 or 6 are chosen.

Perhaps the subalpine and alpine vegetation types in northern Sweden will be more resistant to trampling if they are regularly exposed to relatively extensive grazing.

In many cases there is probably a correlation between biomass/production in a vegetation type and the intensity of grazing. However, several examples in the literature indicate the opposite. In northern Sweden and Finland there are indications of at least a rough correlation between grazing and production. Perhaps that is why resistance to trampling in many of these vegetation types is more an adaptation to grazing than to trampling. High productivity counteracts the effects of herbivory by, e.g., replacing wounded parts of the plants.

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5. REFERENCES

- Bates, G.H. 1935. The vegetation of footpaths, sidewalks, cart-tracks and gateways. *J.Ecol.* 25 469-81.
- Bates, G.H. 1938a. The vegetation of wayside and hedgerow. *J. Ecol.* 25 469-81.
- Bates, G.H. 1938b. Life forms of pasture plants in relation to treading. *J.Ecol.* 26 452-55.
- Bates, G.H. 1951. Track making by man and domestic animals. *J. Anim. Ecol.* 20 21-28.
- Bayfield, N.G. 1971. Some effects of walking and skiing on vegetation at Cairngorm. In: *The Scientific Management of Animal and Plant Communities for Conservation* (Ed. E. Duffey and A.S Watt), pp. 469-85. Blackwell Scientific Publications, Oxford.
- Bayfield, N. 1979. Recovery of four montane heath communities on Cairngorm, Scotland, from disturbance by trampling. *Biol. Conserv.*, 15:165-79.

- Blom, C.V.P.M. 1979. Effects of trampling and soil compaction on the occurrence of some Plantago species in costal sand dunes. - Thesis, Univ. of Nijmegen 1979.
- van den Brink, F.H. 1958. Alla Europas däggdjur. - Stockholm.
- Bryan, R. 1977. The impact of recreational use on the Swedish mountain landscape. Geografiska Annaler, Vol 59a 1-2 .
- Dale, D. & Weaver, T. 1974. Trampling effects on vegetation of the trail corridors of North Rocky Mountain forests. J. appl. Ecol. 11 767-72.
- Emanuelsson, U. 1978. Mekanisk påverkan på växttäcket inom hedartade ekosystem i fjällterräng. Rapport över förundersökning. -Dept. of Plant Ecology, Univ. of Lund (mimeo.).
- Emanuelsson, U. 1979. A method for measuring trampling effects on vegetation (The circle sector method). -In:Proceedings from Oikos/NKE-conference 1979.
- Emanuelsson, U. 1984a. Vegetation zonation on tracks through dwarf shrub heaths in the Torneträsk area, northern Sweden. - Dept. of Plant Ecology, Univ. of Lund (In manuscript).
- Emanuelsson, U. 1984b. Dynamics of dwarf shrub heaths in relation to grazing of small rodents in the Torneträsk area, northern Sweden. - Dept. of Plant Ecology, Univ. of Lund (In manuscript).
- Harper, J.L. 1977. Population Biology of Plants. Academic Press.
- Karlsson, L. 1974. Turistslitage i nedre Rapadalen, Sareks nationalpark. Meddelande från Växtbiologiska inst., Uppsala, Nr 7.
- Kellomäki, S. 1973. Ground cover response to trampling in a spruce stand of Myrtillus type. -Silva Fennica 7:2, 96-113.
- Kellomäki, S. 1977. Deterioration of forest ground cover during trampling. -Silva Fennica 11 153-61.
- Kellomäki, S. & Saastamoinen, U.-L. 1975. Trampling tolerance of forest vegetation. - Acta Forestalia Fennica 147.
- Krok, T.O.B.N. & Almquist, S. 1962. Svensk flora för skolor. Kryptogamer. 25 uppl. - Stockholm.
- Lid, J. 1974. Norsk og svensk flora. 2 uppl. - Oslo.

- Liddle, M.J. 1975a. A selective review of the ecological effects of human trampling on natural ecosystems. -Biol. Conserv. 7 17-36.
- Liddle, M.J. 1975b. A theoretical relationship between the primary productivity of vegetation and its ability to tolerate trampling. Biol Conserv. 8:251-255.
- Liljelund, L-E., Emanuelsson, U., Florgård, C. and Hofman-Bang, V. 1977. Kunskapsöversikt och forskningsbehov rörande mekanisk påverkan på mark och vegetation. Meddelande Nr 79/4 från Botaniska Institutionen vid Stockholms Univesitet (mimeo.).
- Mårtensson, O. 1956. Bryophytes of the Torneträsk area, northern Swedish Lapland. LLL. General part. - K. Sv. Vet. Akad. Avhandl. i Naturskyddsärenden 15, 94 pp.
- Sandberg, G 1963. Växtvärlden i Abisko nationalpark. In: Curry-Lindahl, C. (ed.). Natur i Lappland, Svensk Natur, Uppsala. pp. 885-909.
- Satchell, J.E. and Marren, P.R. 1976. The effects of recreation on the ecology of natural landscapes. Nature and Environment series No.11 Council of Europe.
- Simpson, E.H. 1949. Measurement of diversity. - Nature 163:688.
- Sjörs, H. 1956. Nordisk växtgeografi. -Stockholm.
- Shimwell, D.W. 1971. Description and Classification of Vegetation. - London.
- Sokal, R.R. & Rohlf, F.J. 1969. Biometry. The principles and practice of statistics in biological research. - San Francisco.
- Sonesson, M. 1967. Studies on mire vegetation in the Torneträsk area, Northern Sweden. I. Regional aspects. - Botaniska Notiser 120:272-296.
- Sonesson, M. 1970. Studies on mire vegetation in the Torneträsk area, Northern Sweden. III. Communities of the poor mires. - Opera Botanica 26:120 pp.
- Sonesson, M. 1980. Klimatet och skogsgränsen i Abisko. -Fauna och Flora Årg 75:1.
- Sonesson, M. & Lundberg, B. 1974. Late Quarternary forest development of the Torneträsk area, North Sweden. I. Structure of modern forest ecosystems. - Oikos 25:121-133.

- Streeter, D.T. 1971. The effects of public pressure on the vegetation of chalk downland at Box Hill, Surrey. -In: The Scientific Management of Animal and Plant Communities for Conservation. (Ed. by E. Duffey and A.S. Watt), pp. 459-68. Blackwell Scientific Publications, Oxford.
- Vegetationskartor över svenska fjällkedjan. 1979-84. Liber Kartor, Stockholm.

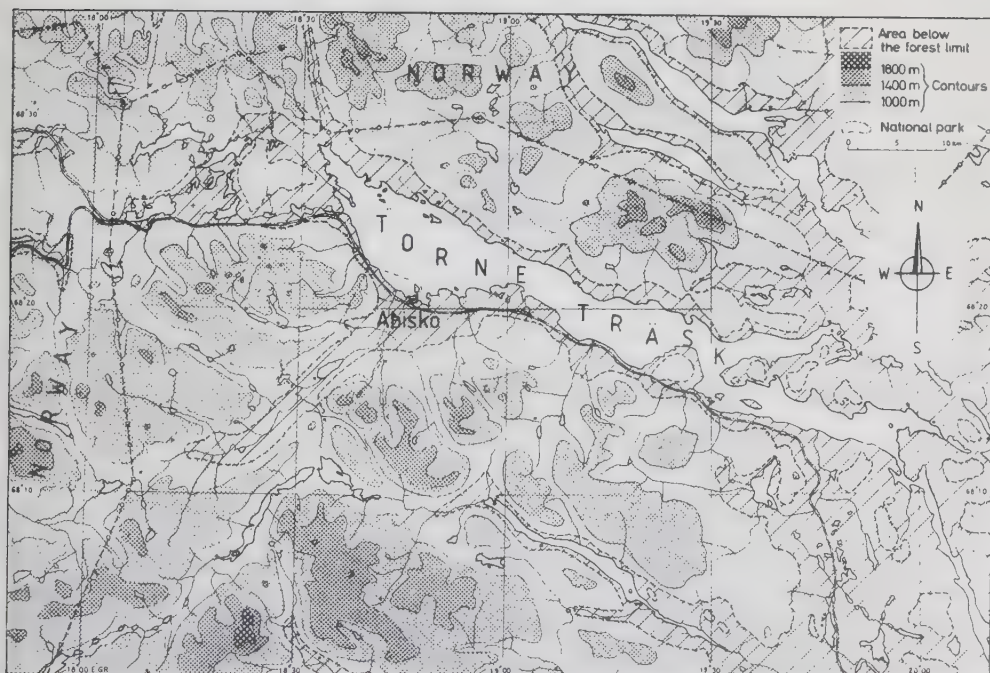
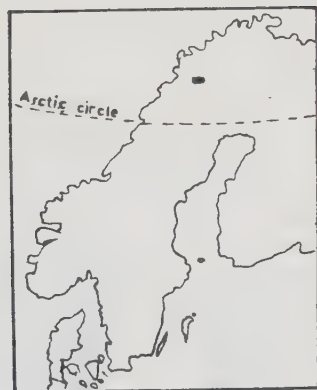
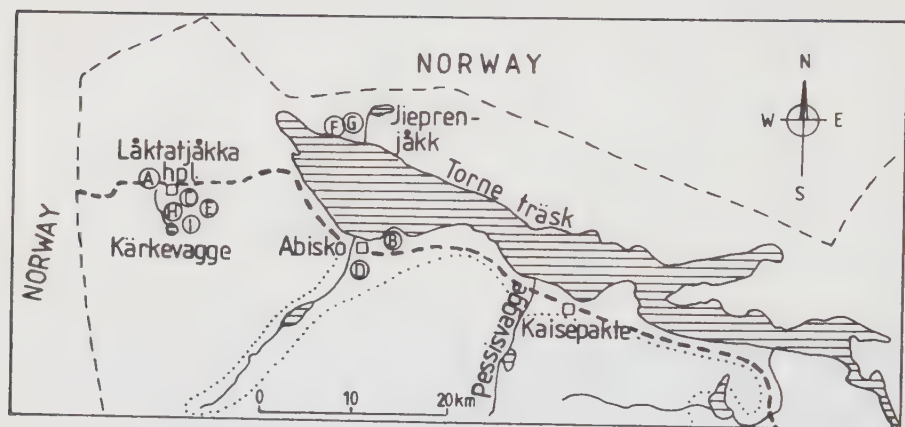
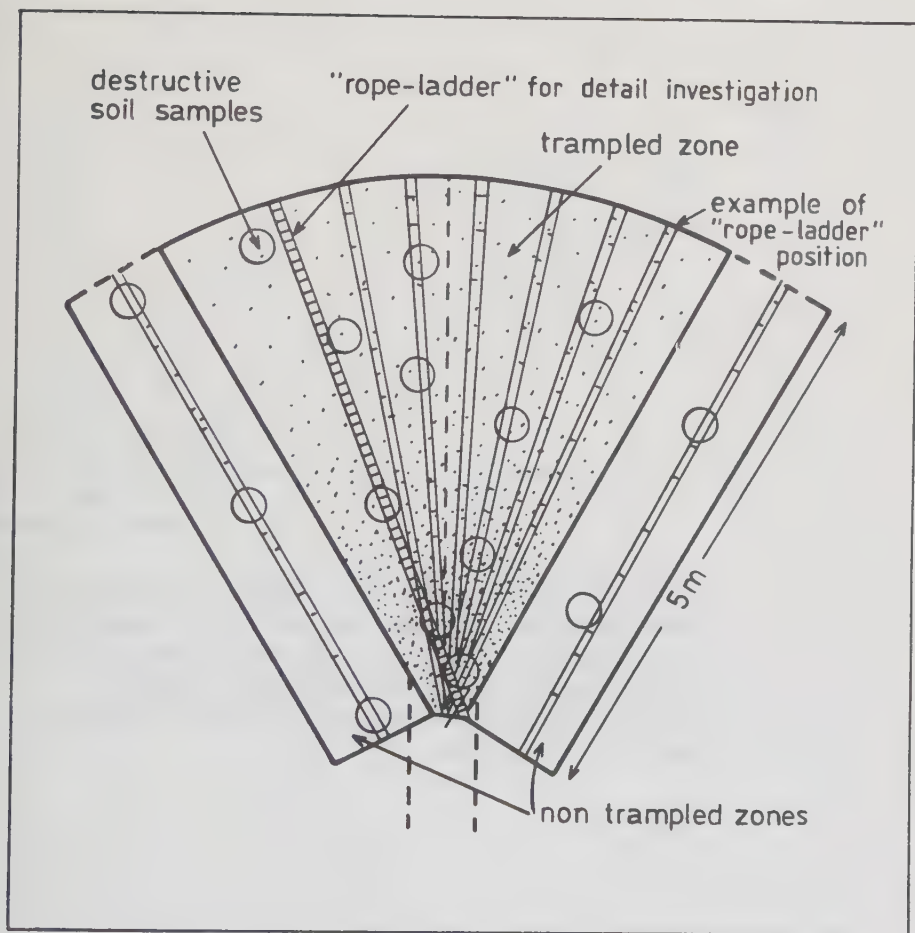


Fig 1a.

Map of the Torneträsk area (adapted from Sonesson & Lundberg 1974).----- = tree-line.



2. The Torneträsk area with the positions of the experimental sites described in Table 1.

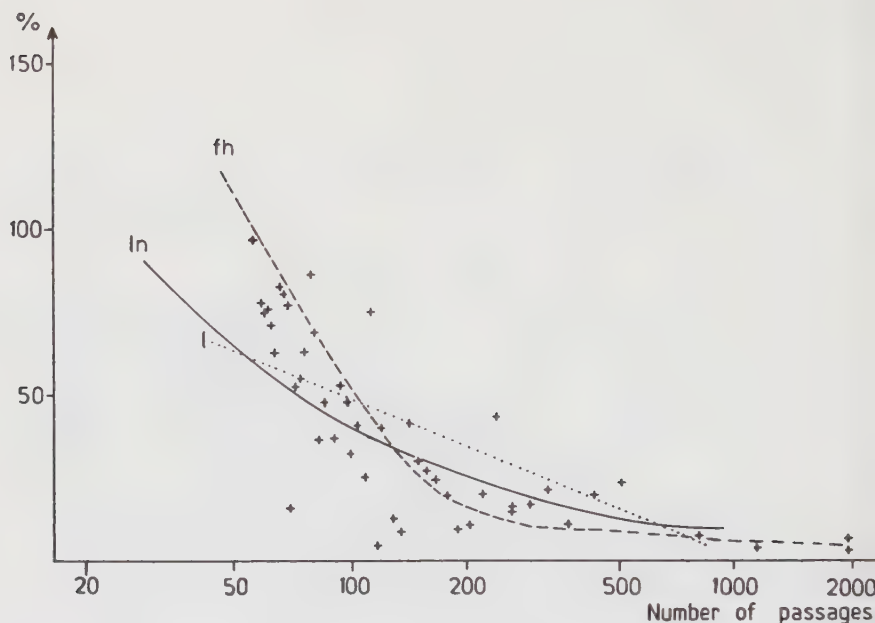


3. Design of the trampling device, shaped like a circle sector.

Experimental trampling was performed by walking from the tip to the arc of the circle sector and back again 100 times while changing the arrival point on the arc 5 cm each time. Non-trampled reference zones are shown, as well as the positions of the "rope-ladder" described in the text.

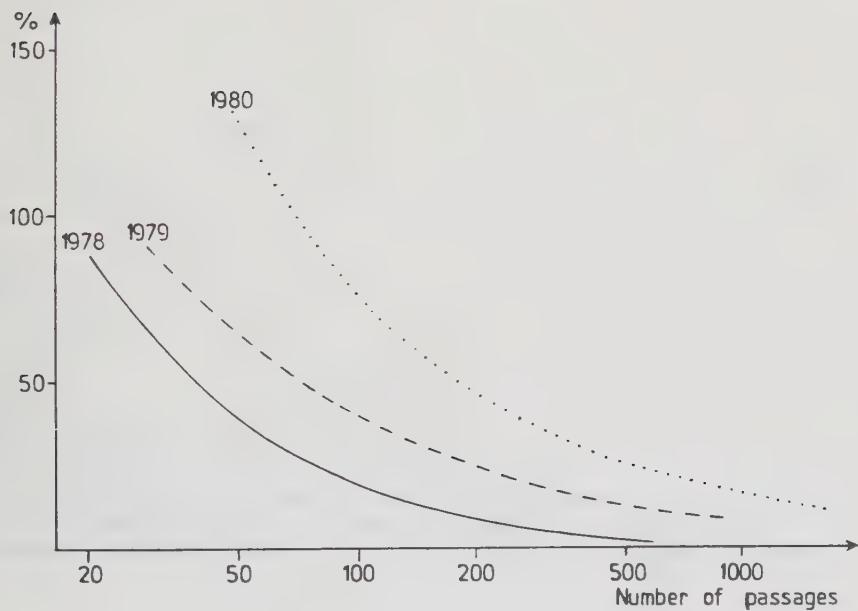
The two positions of the "rope-ladder" in the reference zones are also indicated.

Positions of soil core samples are indicated.

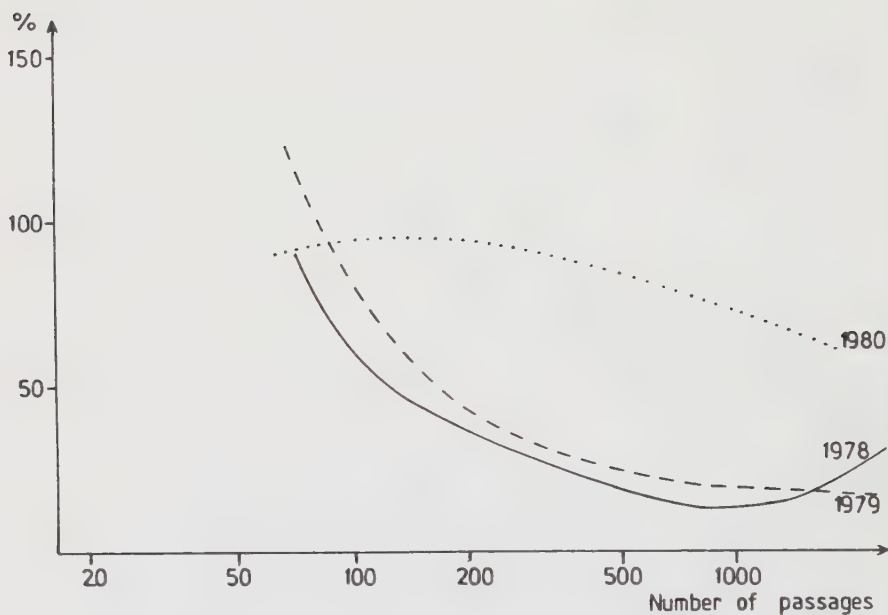


4. The relationship between cover (expressed as percentage of untrampled similar vegetation) and quantity of trampling in one plot dominated by *Empetrum*-vegetation trampled in July 1978 and measured in early September, 1979 (Example).

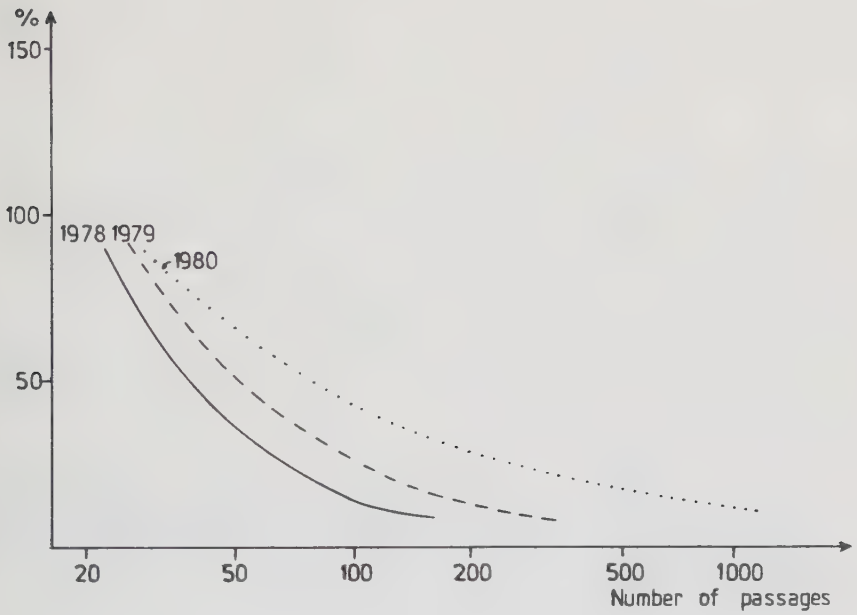
(l) linear regression, (ln) natural logarithmical regression, and (fh) fitted by hand.



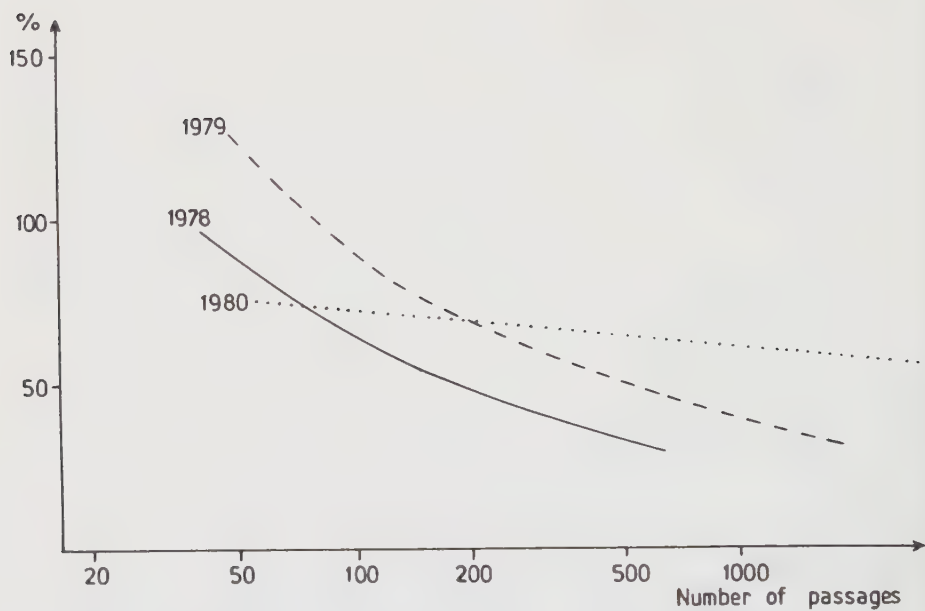
5a. The relationship between amount of trampling in 1978 and the effects on cover in 1978, 1979, and 1980 (the cover is expressed as percentage of untrampled similar vegetation). *Empetrum*-dominated vegetation trampled on one occasion in mid July, 1978. Example from site C, circle sector 11 (cf. Fig. 3 and Table 1).



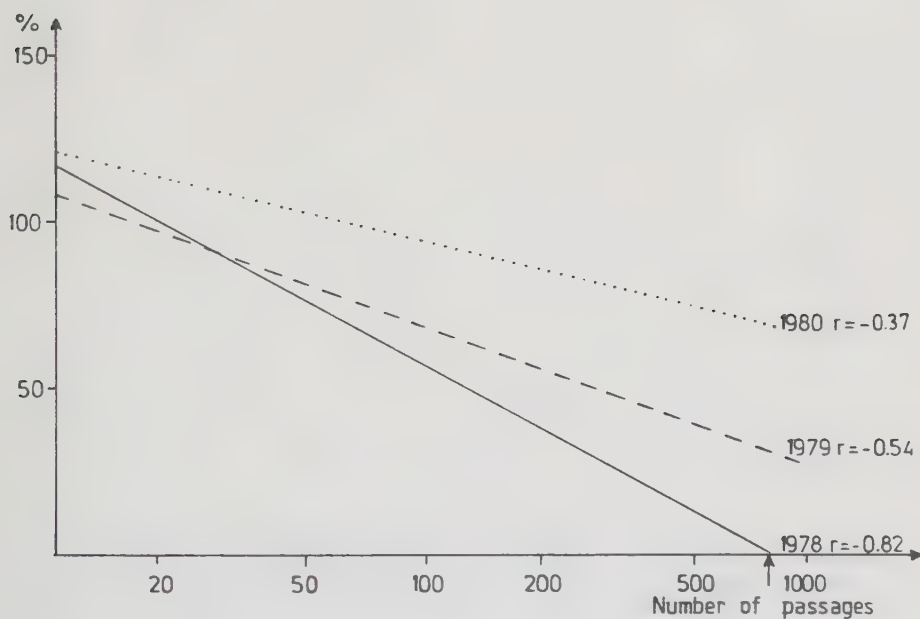
5b. Dryas-dominated vegetation trampled on one occasion in mid July. Example from site I, circle sector 26.



5c. *Empetrum*-dominated vegetation trampled on three occasions during the summer. Example from site C, circle sector 13.

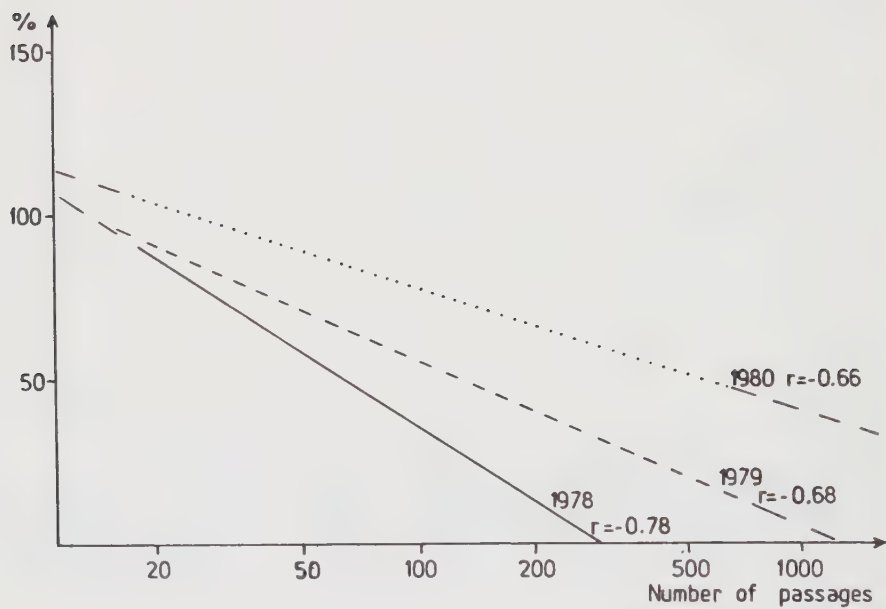


5d. Low-herb meadow trampled on one occasion during mid July.
Example from site H, circle sector 23.

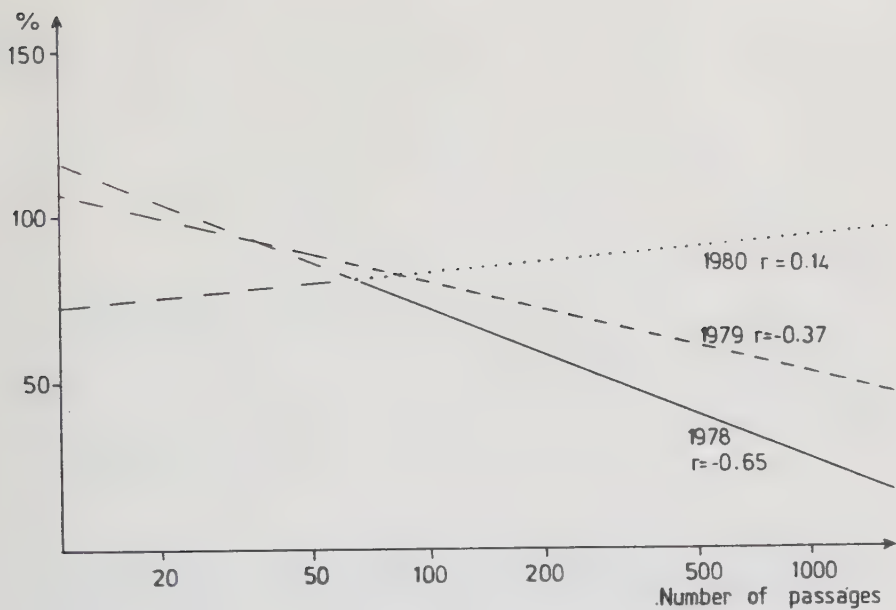


6a. Relationship between amount of trampling in 1978 and the numbers of species in 1978, 1979 and 1980 (expressed as percentage of the number of species in similar untrampled vegetation).

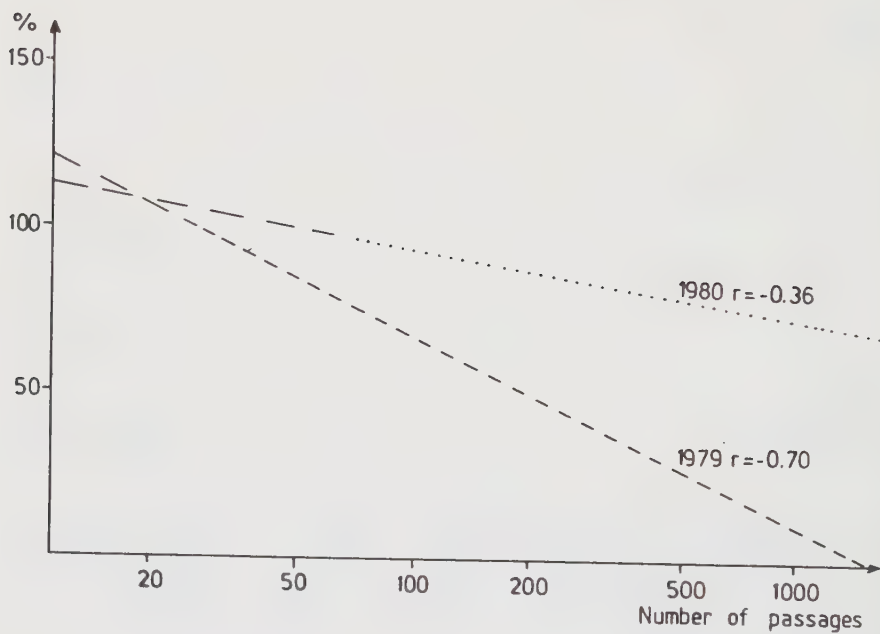
Fen trampled on one occasion in mid June 1978. Example from site A, circle sector 2.



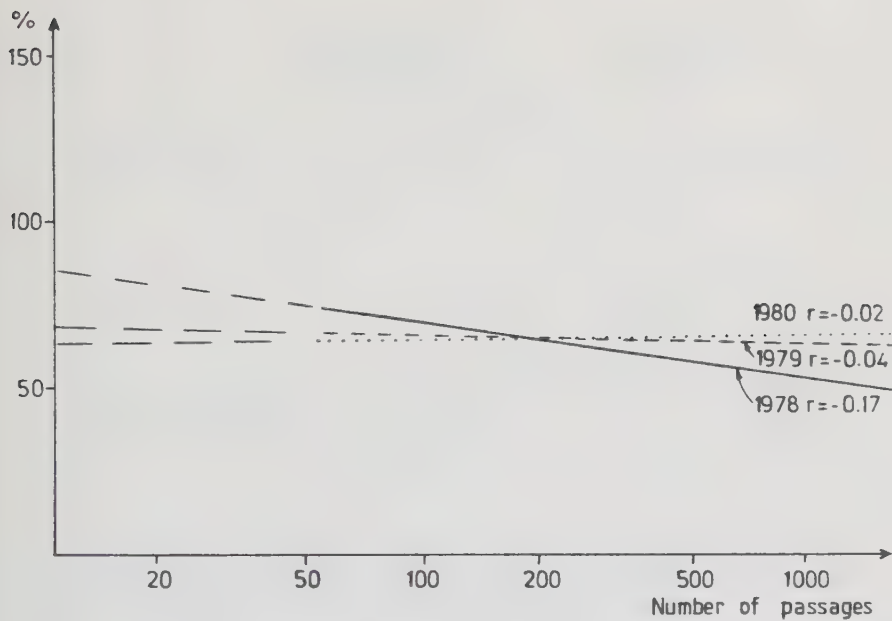
6b. Fen trampled on one occasion in mid July. Example from site A, circle sector 3.



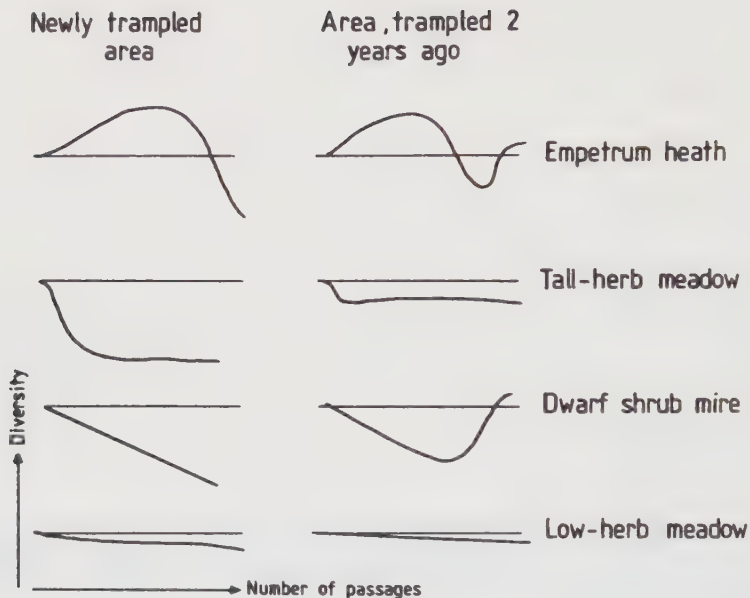
6c. *Empetrum*-dominated vegetation trampled on one occasion in mid August. Example from site C, circle sector 12.



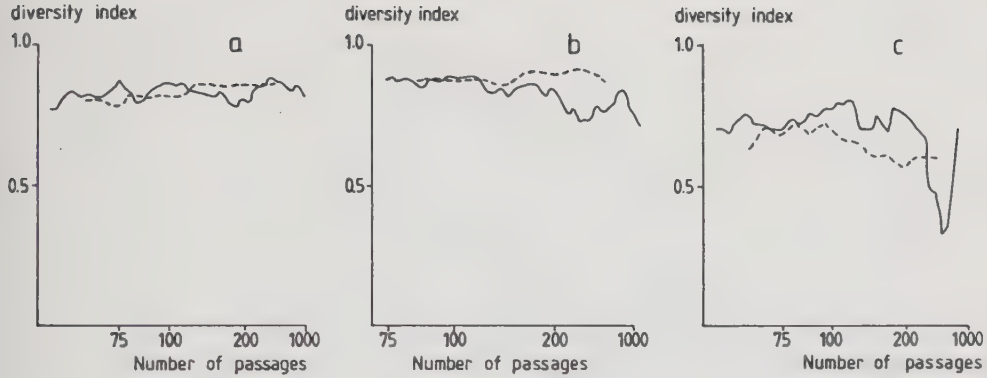
6d. Middle alpine grass-heath trampled every day throughout the summer, 1979. Example from the Tarfala valley, circle sector 29.



6e. Dryas-dominated vegetation trampled on one occasion in mid July. Example from site I, circle sector 26.



7.Changes in diversity (Simpsons index) in relation to increased trampling in different vegetation types. On the x-axis is increased amount of trampling showed, on the y-axis is the diversity showed. The straight, thinner line represents the mean diversity in untrampled vegetation while the thicker line represents the trampled vegetation. Principle diagrams, summarizing the result of 30 plots studied during 1978-80.

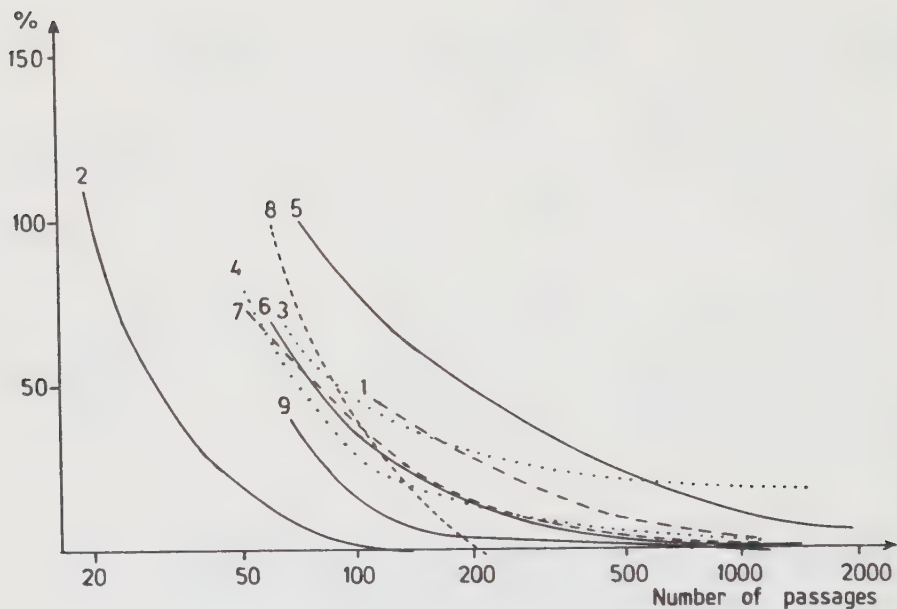


8. The relationship between amount of trampling and diversity in plant communities. Solid line represents samples from the circle sectors and the dotted lines represent the same positions in the non-trampled reference zones.

a. Low-herb meadow after 1 month.

b. Low-herb meadow after 3 months.

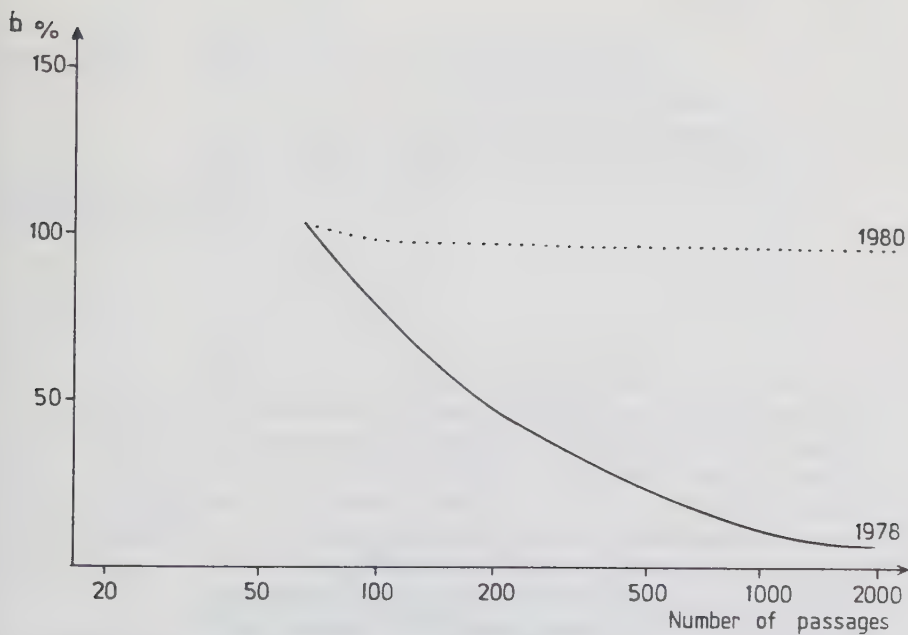
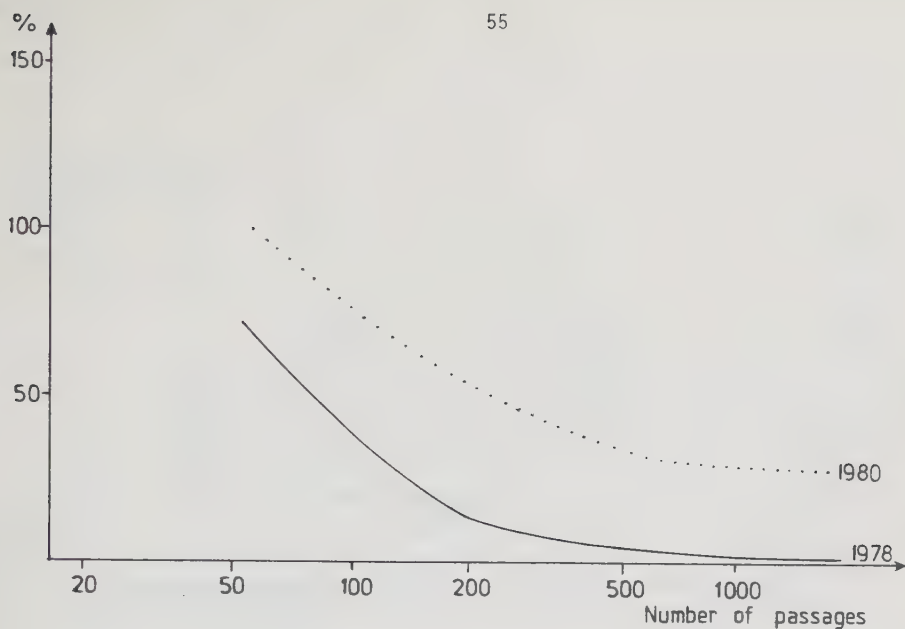
c. Empetrum-dominated vegetation 3 months after trampling.



9. Relationship between trampling and above-ground plant biomass expressed as percentage of biomass in untrampled similar vegetation (the non-trampled reference zones).

The trampling was performed in mid July 1978 and the samples were taken in early September the same year.

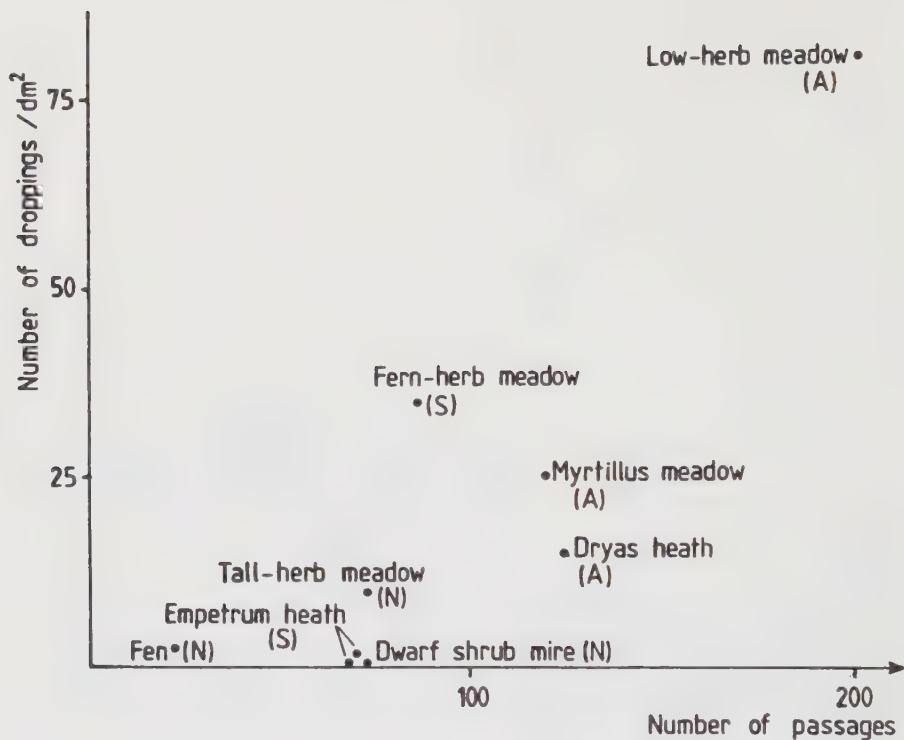
1=Herb-fern meadow, 2=Fen, 3=Dryas heath, 4=Myrtillus meadow, 5=Low-herb meadow, 6=Dwarf shrub mire, 7=Empetrum heath, 8=Myrtillus heath, 9=Tall-herb meadow.



10. Relationship between trampling and above-ground plant biomass. The biomass is expressed as the percentage of the biomass in the non-trampled reference zones.

a. *Empetrum*-dominated vegetation.

b. Low-herb meadow.



11. The relationships between trampling resistance of the vegetation and the number of small rodent droppings in 1978. The trampling resistance is expressed as the number of passages in the middle of the summer that the vegetation types are capable of withstanding without having lost more than 50% of the original cover the end of the summer. Values taken from the first row in Table 4 (FH 1978). Observations (June-September 1978) of grazing reindeers at the same sites was also noted. A=abundant, S=scarce, N=never observed.

Table 1. Some background information on the sites where the circle sectors were placed.

Name of veg. type in the present paper.	Structurally important species, according to the vegetation- circle sectors at map of the Swedish mountains (Vegetationskartor 1979-1984)	Code for the vegetation- circle sectors	Location	Code for the sites in Fig. 2.	Altitude (m)	Annual precipitation	Soil	Biomass g/m ² (s. d) Aug 1978
Fen	<i>Andromeda polifolia</i> <i>Scirpus caespitosus</i> <i>Sphagnum</i> spp.	1,2,3,4	Läktatjåkka hpl	A	500	807**	Sphagnum-Carex peat	282 ± 47
Dwarf shrub mire	<i>Empetrum hermaphroditum</i> <i>Sphagnum</i> spp.	5,6,7,8,9	Abisko	B	360	300	Sphagnum peat/peat soil	437 ± 145
Empetrum heath	<i>Empetrum hermaphroditum</i> <i>Vaccinium vitis-idaea</i>	10,11,12, 13,14	Kärkevage	C	600	807*	stony loam with 4 cm layer of peat/podsol	778 ± 88
Empetrum heath	<i>Empetrum hermaphroditum</i> <i>Vaccinium vitis-idaea</i> with mosses	15,16	Abisko	D	400	300	stony sand/podsol	-
Myrtillus heath	<i>Empetrum hermaphroditum</i> <i>Vaccinium myrtillus</i> with mosses	17	Abisko	D	400	300	stony till/podsol	522 ± 177
Myrtillus meadow	<i>Vaccinium myrtillus</i> <i>Anthoxanthum odoratum</i> <i>Phleum commutatum</i>	18	Kärkevage	E	670	807*	stony loam/brown earth soil	347 ± 83
Tall-herb meadow	<i>Geranium silvaticum</i> <i>Trollius europaeus</i>	19,20	Jiepreknedde	F	360	518***	coarse sandy loam/ gley soil	290 ± 241
Fern-herb meadow	<i>Gymnocarpium dryopteris</i> <i>Rumex acetosa</i>	21	Jiepreknedde	G	370	518***	coarse sandy loam/ brown earth soil	193 ± 85
Low-herb meadow	<i>Polygonum viviparum</i> <i>Ranunculus</i> spp. Poaceae	22,23,24,25	Kärkevage	H	630	807**	stony loam/ brown earth soil	142 ± 65
Dryas heath	<i>Dryas octopetala</i> Extremely dry heath (Rich vegetation)	26	Kärkevage	I	650	807**	stony loam/ rezina soil	325 ± 79
Middle alpine heath	Mosses and lichens <i>Empetrum hermaphroditum</i>	27,28	Tarfala	-	1200	950	stony till/podsol-like soil	-
Middle alpine meadow	<i>Carex bigelowii</i> Grass heath	29,30	Tarfala	-	1200	950	stony till/ brown earth-like soil	-

* 400 m south of Tarfala Scientific Research Station approx. 100 km south of Abisko.
** Katterjåkk
*** Mean value for 1973-81

Table 2. Vegetation of the untrampled reference zones of the circle sectors used for the investigation (cf. Fig. 2). The first figure shows the percentage frequency of the species in the 17 investigated sub-plots (1dm²), the second figure shows the mean cover.

a. Circle sectors 1-26 placed in the sub-alpine and the low alpine belts. Species are arranged to get a diagonal of figures through the diagram.

b. Circle sectors 27-30 found in the middle alpine belt. Species are arranged in bigger taxonomic groups and in alphabetical order.

CIRCLE SECTOR NUMBER:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>Scirpus caespitosus</i>	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²	100 ²²
<i>Carex lasiocarpa</i>	65 ¹²	53 ¹²	41 ²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	65 ¹²	
<i>Sphagnum fuscum</i>	59 ³⁰	71 ²⁶	65 ²⁰	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	65 ²⁶	
<i>Sphagnum</i> spp.	23 ¹²	12 ²																								
<i>Tomentypnum nitens</i>	53 ¹⁰	53 ¹¹	94 ¹¹	64 ¹²																						
<i>Oxycoccus microcarpus</i>	6 ²																									
<i>Andromeda polifolia</i>	82 ¹¹	88 ¹¹	94 ¹⁰	70 ¹⁰	94 ¹⁰	82 ²	88 ²	82 ²	71 ²																	
<i>Potentilla palustris</i>	24 ¹⁰																									
<i>Drepanocladus intermedius</i>	53 ²⁶	65 ²²	35 ¹²	35 ²⁶																						
<i>Betula nana</i>	41 ¹²	18 ¹²																								
<i>Empetrum hermaphroditum</i>	12 ¹²																									
<i>Vaccinium uliginosum</i>	35 ²	29 ²	24 ²	29 ²	29 ²	65 ²	24 ²	24 ²	59 ¹²																	
<i>Rubus chamaemorus</i>	88 ²	94 ¹²	71 ¹²	82 ¹²	88 ¹²																					
<i>Cetraria nivalis</i>	71 ¹¹	76 ¹²	82 ¹²	59 ²¹	71 ¹²																					
<i>Dicranum</i> spp.	6 ¹⁰																									
<i>Cladonia</i> spp.	6 ²⁰	6 ²																								
<i>Cetraria islandica</i>																										
<i>Vaccinium vitis-idaea</i>																										
<i>Nephroma arcticum</i>																										
<i>Stereocaulon pascale</i>																										
<i>Peltigera</i> spp.																										
<i>Pleurozium schreberi</i>																										
<i>Polytrichum</i> spp.																										
<i>Arctostaphylos alpina</i>																										
<i>Carex bigelowii</i>																										
<i>Hylocomium splendens</i>																										
<i>Hepaticae</i> spp.																										
<i>Tannohia vermicularis</i>																										
<i>Cornus suecica</i>																										
<i>Vaccinium myrtillus</i>																										
<i>Deschampsia flexuosa</i>																										
<i>Festuca ovina</i>																										
<i>Equisetum pratense</i>																										
<i>Linnæa borealis</i>																										
<i>Lycopodium annotinum</i>																										

<i>Alchemilla</i> spp.	6 ²	12 ¹⁰	6 ²⁰	12 ¹⁰	6 ¹⁰	35 ¹³	82 ¹³	6 ¹⁰
<i>Polygonum viviparum</i>			76 ⁷		29 ²	76 ¹²	76 ⁶	53 ²⁴
<i>Rumex acetosa</i>			18 ⁴	24 ²³	18 ²³	29 ¹⁴	6 ²	18 ¹²
<i>Anthoxanthum odoratum</i>			94 ¹⁰		76 ¹¹	53 ⁷	76 ¹⁰	65 ⁵⁹
<i>Ranunculus acris</i>			76 ⁴		12 ²	29 ²	47 ⁷	47 ⁷
<i>Salix herbacea</i>			53 ⁷		41 ¹⁰	65 ¹²	71 ¹³	76 ¹³
<i>Viola biflora</i>			12 ¹⁴		100 ¹³	76 ²⁴	35 ³	85 ¹³
<i>Sibbaldia procumbens</i>			24 ³		12 ¹⁴	71 ⁷	53 ⁷	18 ⁷
<i>Veronica fruticans</i>					41 ³	24 ⁶	6 ²	6 ²
<i>Graphium supinum</i>					12 ²			18 ²
<i>Potentilla crantzii</i>			6 ²					
<i>Pyrola minor</i>			6 ²					
<i>Saussurea alpina</i>			12 ²		6 ¹⁰	12 ²	35 ³	6 ¹⁰
<i>Geranium silvaticum</i>			6 ¹⁰	12 ²³	6 ²⁰	24 ³	12 ¹³	12 ²⁰
<i>Filipendula ulmaria</i>				94 ¹⁴	88 ¹¹	82 ²³		
<i>Roegneria borealis</i>				59 ²²				
<i>Poa nemoralis</i>				59 ¹²	35 ⁷			
<i>Valeriana officinalis</i>				35 ⁷	18 ¹			
<i>Solidago virgaurea</i>				35 ¹⁷	18 ¹⁰			
<i>Geum rivale</i>				29 ³⁴	47 ¹⁷	65 ¹⁹		
<i>Rubus saxatilis</i>				6 ³⁰				
<i>Stellaria nemorum</i>				53 ²⁴	12 ²⁰			
<i>Melampyrum sylvaticum</i>				6 ¹				
<i>Chamaenerion angustifolium</i>				12 ²	18 ²	18 ⁷		
<i>Equisetum palustre</i>				6 ¹⁰				
<i>Melandrium rubrum</i>				6 ²	18 ²	12 ¹		18 ²
<i>Troilus europaeus</i>				20 ²				
<i>Gymnocarpium dryopteris</i>				47 ²³	6 ¹⁰			
<i>Mucedium alpinum</i>				6 ¹⁴	53 ²¹			
<i>Rhytidium</i> spp.				6 ²⁰				
<i>Rhyzodadelphus</i> spp.								
<i>Hieracium alpinum</i>				71 ²	59 ¹²	24 ²	59 ¹²	24 ²
<i>Taraxacum</i> spp.				18 ¹³	35 ³	24 ³		
<i>Juncus trifidus</i>				6 ²	6 ²			
<i>Botrychium lunaria</i>				6 ²				
<i>Festuca rubra</i>				6 ¹	59 ²	24 ²		
<i>Carex capillaris</i>				12 ²				
<i>Dryis octopetala</i>								
<i>Saxifraga oppositifolia</i>								
<i>Asragalus alpinus</i>								
<i>Prepanocladus</i> spp.								
<i>Thalictrum alpinum</i>								
<i>Salix reticulata</i>								
<i>Selaginella selaginoides</i>								
<i>Dicranella</i> spp.								
<i>Carex rupestris</i>								
<i>Stene acaulis</i>								
<i>Tortula</i> spp.								
<i>Tortula pusilla</i>								

Table 2b

	Circle sector:	27	28	29	30
<i>Arctostaphylos alpina</i>		12-25			
<i>Bartsia alpina</i>			6-5		
<i>Diapensia alpina</i>		6-20			
<i>Cassiope hypnoides</i>		59-13	71-15	6-10	6-5
<i>Dryas octopetala</i>		12-15	18-20		
<i>Empetrum hermaphroditum</i>		24-28			
<i>Loiseleuria procumbens</i>		6-10			
<i>Polygonum viviparum</i>		18-5	30-6	24-5	
<i>Potentilla crantzii</i>				29-6	
<i>Ranunculus nivalis</i>				18-5	
<i>Salix herbacea</i>		47-11	67-9	94-8	59-10
<i>Thalictrum alpinum</i>				47-6	
<i>Vaccinium uliginosum</i>		41-20	12-12		
<i>Vaccinium vitis-idaea</i>		12-8		65-7	35-10
<i>Agrostis borealis</i>		41-6			12-5
<i>Carex bigelowii</i>		35-8	65-10	94-11	100-16
<i>Festuca alpina</i>		6-5	30-13	100-11	53-8
<i>Juncus biglumis</i>		29-6			
<i>Juncus trifidus</i>		6-20			
<i>Lycopodium alpinum</i>					12-5
<i>Dicranum</i> spp.		59-10	29-5	65-7	41-5
<i>Hepaticae</i>		6-5	18-7	6-5	
<i>Hylocomium splendens</i>				65-10	
<i>Polythricum</i> spp.			30-5		82-7
<i>Pleurozium schreberi</i>			24-5		
<i>Alectoria ochroleuca</i>		12-8			
<i>Cetraria islandica</i>		53-6	76-8	35-5	59-5
<i>Cetraria nivalis</i>		59-10	36-5		
<i>Cladonia</i> spp.		24-5	70-6	82-17	70-5
<i>Lecanora</i> spp.		47-14	82-14		
<i>Solorina crocea</i>		6-5	12-7		
<i>Sphaerophorus globosus</i>		35-5			
<i>Stereocaulon paschale</i>			41-7	12-5	65-7
<i>Thamnochloa vermicularis</i>		76-10	6-10		24-5

Table 3. General design of the experiment.

a. Dates and amounts of trampling.

b. Dates of investigation.

Table 3a.

Circle

sector

	770815	780615	780701	780715	780801	780815	790715	64 days in 1979
1		1600						
2		533						
3				533				
4						533		
5		1600						
6				1600				
7						1600		
8		533		533		533		
9		320	320	320	320	320		
10		1600						
11				1600				
12						1600		
13		533		533		533		
14		320	320	320	320	320		
15	1600							
16								25
17				1600				
18				1600				
19		1600						
20				1600				
21				1600				
22		1600						
23				1600				
24						1600		
25		533		533		533		
26				1600				
27							1600	
28								25
29							1600	
30								25

Table 3b.

Circle sector	Biomass/ soil samples Sept 78	Time of surveying the circle sectors		
		Sept 78	Sept 79	Sept 80
1		X	X	X
2		X	X	X
3	X	X	X	X
4		X	X	X
5		X	X	
6	X	X	X	
7		X	X	
8		X	X	
9		X	X	
10		X	X	X
11	X	X	X	X
12		X	X	X
13		X	X	X
14		X	X	X
15		X	X	X
16			X	X
17	X	X	X	X
18	X	X	X	X
19		X	X	X
20	X	X	X	X
21	X	X	X	X
22		X	X	X
23	X	X	X	X
24		X	X	X
25		X	X	X
26	X	X	X	X
27			X	X
28			X	X
29			X	X
30			X	X

4. The number of passages required in 1978 to reduce the cover of the vegetation to 50% of untrampled vegetation in 1978, 1979 and 1980. The figures are extracted from correlation diagrams of the type drawn in Figs. 4 and 5.

The diagrams are fitted either by hand (FH), (4a), linearly (L), (4b) or logarithmically (LN), (4c).

For (LN) and (L) it is possible to give the 95% confidence interval.

1600 is the largest number of passages used in the experiment.

4a.(FH), fitted by hand

circle sector	78	79	80
Fen			
1	47	74	78
2	26	30	40
3	22	29	31
4	28	55	395
Dwarf shrub mire			
5	115	>1600	-
6	72	>1600	-
7	75	103	-
8	78	108	-
9	80	83	-
Empetrum heath			
10	67	98	493
11	68	92	358
12	72	99	245
13	62	75	84
14	47	81	299
15	90	492	148
16		122	230
Myrtillus heath			
17	70	70	284
Myrtillus meadow			
18	119	164	245
Tall-herb meadow			
19	347	>1600	>1600
20	72	>1600	>1600
Fern-herb meadow			
21	86	>1600	-
Low-herb meadow			
22	>1600	>1600	>1600
23	200	403	1590
24	48	400	1054
25	116	513	>1600
Dryas heath			
26	125	167	>1600
Middle alpine heath			
27		137	200
28		79	140
Middle alpine grass heath			
29		330	578
30		85	340

4b. (L), linear fitting, in brackets 95% confidence interval.

circle
sector

	78	79	80
Fen			
1	4 (2-5)	65 (45-92)	146 (92-233)
2	17 (14-21)	39 (31-49)	400 (260-616)
3	12 (10-15)	51 (39-68)	48 (37-63)
4	10 (8-12)	78 (62-98)	842 (515-1378)
Dwarf shrub mire			
5	218 (145-327)	>1600	-
6	64 (46-90)	136 (106-176)	-
7	13 (9-19)	79 (61-100)	-
8	63 (39-104)	167 (119-223)	-
9	65 (42-99)	71 (54-93)	-
Empetrum heath			
10	35 (28-44)	187 (132-266)	942 (701-1266)
11	12 (10-15)	92 (70-121)	461 (317-670)
12	1 (1-2)	122 (88-170)	978 (651-1471)
13	6 (5-7)	38 (30-48)	103 (73-146)
14	3 (2-3)	83 (61-112)	
15	100 (71-141)	1067 (675-1600)	271 (175-421)
16		155 (107-223)	316 (201-497)
Myrtillus heath			
17	63 (47-86)	56 (41-75)	425 (215-839)
Myrtillus meadow			
18	164 (130-206)	331 (235-466)	1089 (725->1600)
Tall-herb meadow			
19	506 (380-675)	>1600	>1600
20	11 (8-15)	>1600	>1600
Fern-herb meadow			
21	32 (25-41)	1600	-
Low-herb meadow			
22	>1600	>1600	>1600
23	288 (199-418)	837 (544-1287)	>1600
24		1272 (903->1600)	>1600
25	206 (146-291)	1271 (830->1600)	>1600
Dryas heath			
26	291 (156-543)	305 (205-452)	>1600
Middle alpine heath			
27		244 (156-382)	>1600
28		95 (68-133)	277 (155-494)
Middle alpine grass heath			
29		534 (397-718)	468 (366-600)
30		119 (87-161)	525 (342-806)

4c. (LN). logarithmical fitting, in brackets 95% confidence interval.

circle sector	78	79	80
Fen			
1.	24 (17-33)	56 (39-81)	83 (60-115)
2.	20 (17-24)	27 (22-34)	100 (82-121)
3.	18 (14-22)	33 (27-40)	34 (30-39)
4.	20 (17-24)	55 (49-62)	325 (277-382)
Dwarf shrub mire			
5.	134 (106-170)	>1600	-
6.	59 (45-78)	103 (82-130)	-
7.	23 (15-35)	80 (63-101)	-
8.	42 (27-65)	114 (93-141)	-
9.	60 (39-91)	79 (60-105)	-
Empetrum heath			
10.	39 (31-48)	119 (93-152)	556 (483-642)
11.	36 (28-47)	72 (57-91)	176 (117-267)
12.	17 (12-23)	82 (55-122)	682 (543-858)
13.	37 (26-52)	51 (39-68)	77 (55-103)
14.	22 (15-32)	75 (58-100)	
15.	78 (60-102)	653 (494-865)	162 (128-204)
16.		109 (82-144)	173 (125-238)
Myrtillus heath			
17.	68 (51-91)	49 (39-61)	153 (104-225)
Myrtillus meadow			
18.	131 (103-166)	185 (147-234)	571 (466-699)
Tall-herb meadow			
19.	266 (225-314)	>1600	>1600
20.	19 (13-27)	505 (341-750)	>1600
Fern-herb meadow			
21.	42 (33-53)	>1600	-
Low-herb meadow			
22.	1354 (1112->1600)	>1600	>1600
23.	192 (151-244)	515 (418-635)	>1600
24.		1019 (845-1229)	1408 (1209->1600)
25.	140 (116-169)	759 (646-892)	944 (795-1119)
Dryas heath			
26.	159 (119-212)	203 (163-253)	>1600
Middle alpine heath			
27.		148 (119-183)	138 (94-202)
28.		64 (45-92)	135 (98-186)
Middle alpine grass heath			
29.		328 (285-378)	228 (186-279)
30.		95 (75-120)	276 (207-350)

Table 5. The percentage of cover in relation to the cover of untrampled vegetation after 200 passages on three occasions (1978, 1979 and 1980) after the trampling took place. The figures are extracted from diagrams of the type shown in Figs. 4 and 5.

circle sector	(FH)			(LN)		
	78	79	80	78	79	80
Fen						
1.	3	7	18	4	7	25
2.	1	3	23	3	7	37
3.	0	0	8	0	0	10
4.	1	18	60	3	21	58
Dwarf shrub mire						
5.	30	75	-	40	-	-
6.	8	26	-	13	30	-
7.	6	20	-	8	26	-
8.	6	29	-	10	39	-
9.	10	23	-	12	26	-
Empetrum heath						
10.	11	37	67	25	36	69
11.	7	17	69	9	24	44
12.	3	23	55	6	28	56
13.	9	7	15	8	13	28
14.	1	17	57	2	23	-
15.	17	40	64	23	58	45
16.		23	55		19	38
Myrtillus heath						
17.	11	19	58	10	18	49
Myrtillus meadow						
18.	41	46	53	39	49	63
Tall-herb meadow						
19.	65	93	105	55	101	
20.	17	80	97	15	65	79
Fern-herb meadow						
21.	25	72	-	22	67	-
Low-herb meadow						
22.	65	80	65	73	83	73
23.	32	81	95	48	70	70
24.				30	65	80
25.				37	78	87
Dryas heath						
26.	37	42	94	45	50	72
Middle alpine heath						
27.		37	50		45	
28.		21	35		23	39
Middle alpine grass heath						
29.		59	67		55	62
30.		27	62		26	57

Table 6. The largest number of passages that some vegetation types can stand yet are still able to recover totally in respect of cover 2 years after the trampling occasion.

circle			circle		
sector			sector		
	(FH)	(LN)		(FH)	(LN)
Fen			Myrtillus heath		
1.		35	17.	60	18
2.	24	65			
3.	24	18			
4.	55	40			
			Tall-herb meadow		
			19.	110	221
			20.	164	
Empetrum heath			Low-herb meadow		
10.	74	57	22.	85	60
11.	105	70	23.		
12.	81	16	24.		74
13.	57	26	25.	178	134
14.	74				
15.			Dryas heath		
16.			26.	355	

Table 7. The number of passages required to reduce the number of species in the vegetation to 50 % of the same untrampled vegetation on three occasions (1978, 1979 and 1980) after the trampling took place. Extracted figures from linear regressions of the type shown in Fig. 6.

circle
sector

	78	79	80
Fen			
2.	129	281	>1600
3.	65	129	545
4.	134	1130	>1600

Dwarf-shrub mire

5.	>1600	>1600	
6.	391	493	
7.	314	620	
8.	1500	1500	
9.	403	464	

Empetrum heath

10.	735	1130	>1600
11.	164	>1600	>1600
12.	305	1236	>1600
13.	213	812	801
14.	99	992	1274
15.	>1600	>1600	1600
16.		441	1600

Myrtillus heath

17.	308	420	>1600
-----	-----	-----	-------

Myrtillus meadow

18.	>1600	>1600	>1600
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Tall-herb meadow

19.	>1600	>1600	>1600
20.	545	>1600	>1600

Fern-herb meadow

21.	302	1600	
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Low-herb meadow

22.	1188	>1600	>1600
23.	1312	>1600	>1600
24.	854	>1600	>1600
25.	>1600	>1600	>1600

Dryas heath

26.	1480	>1600	>1600
-----	------	-------	-------

Middle alpine heath

27.		699	>1600
28.		90	221

Middle alpine grass heath

29.		1064	>1600
30.		441	>1600

Table 8. The number of species in relation (percentage) to the number of species in untrampled vegetation after 200 passages on three occasions (1978, 1979 and 1980) after the trampling took place. The figures are extracted from regressions of the type shown in Fig. 6.

Circle sector	78	79	80
Fen			
1.			
2.	28	56	86
3.	13	40	66
4.	41	75	85
Dwarf shrub mire			
5.	91	107	
6.	64	64	
7.	58	78	
8.	81	84	
9.	65	83	
Empetrum heath			
10.	68	78	104
11.	47	80	95
12.	58	72	87
13.	52	73	82
14.	34	76	118
15.	96	107	100
16.		77	111
Myrtillus heath			
17.	72	66	93
Myrtillus meadow			
18.	88	93	98
Tall-herb meadow			
19.	69	95	113
20.	53	80	90
Fern-herb meadow			
21.	64	95	
Low-herb meadow			
22.	72	92	96
23.	78	86	104
24.	83	101	105
25.	98	92	100
Dryas heath			
26.	64	65	65
Middle alpine heath			
27.		67	80
28.		37	52
Middle alpine grass heath			
29.		77	94
30.		50	87

Table 9. The maximal number of passages which some vegetation types can stand yet still recovering in terms of number of species after 2 years and some months (1,2 and 3 months). The figures are extracted from regressions of the type shown in Fig. 6.

Circle
sector

Fen		Myrtillus heath	
		17.	121
2.	67		
3.	26	Myrtillus meadow	
4.	60	18.	148
		Tall-herb meadow	
		19.	>1600
		20.	
Empetrum heath		Low-herb meadow	
10.	281	22.	110
11.	67	23.	>1600
12.		24.	>1600
13.	95	25.	200
14.	279		
15.	200	Dryas heath	
16.	>1600	26.	

Table 11. The table shows whether a species is getting relatively more or less common in the vegetation as a result of trampling.

+ = more than .95 positive correlation

(+) = more than .85 positive correlation

- = more than .95 negative correlation

(-) = more than .85 negative correlation

0 = no positive or negative correlations over .85.

The figures are calculated on the cover for each species in relation to the sum of

relation to the sum of cover of all other species.

Ranking according to relative ability to withstand trampling.

[illegible]

Table 12. Summary of different ways to express the vulnerability of investigated vegetation types (cover).

Values from Tables 4 and 5.

The vegetation types are ranked according to vulnerability.

First figure is the value taken from Table 4 or 5.

Exponents show the rank of the vegetation types according to the vulnerability.

I is (FH) the value for the number of passages needed to reduce the cover to 50% some months after the trampling.

II as I, but (LN) values used.

III is the cover in the autumn of the trampling year if 200 passages have occurred in the vegetation. Taken from the curves fitted by hand (FH).

IV is the same as III but using a (LN) curve.

V-VIII as I-IV but values are from surveys in the autumn of the year after trampling.

IX-XII as I-IV but values are from surveys done in the autumn two years after the trampling.

XIII-XV is the mean rank of the vegetation types.

circle sector		1:st year				2:nd year				3:rd year				RANK		
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
2	FEN	22 ¹	18 ¹	0 ¹	0 ¹	29 ¹	33 ¹	0 ¹	0 ¹	31 ¹	34 ¹	8 ¹	10 ¹	1	1	1
11	EMPETRUM HEATH	68 ²	36 ³	7 ²	9 ²	92 ³	72 ³	17 ²	24 ³	358 ⁴	176 ³	69 ⁴	44 ²	2	3	4
17	MYRTILLUS HEATH	70 ³	68 ⁶	11 ⁴	10 ³	70 ²	49 ²	19 ³	18 ²	284 ³	153 ²	58 ³	49 ³	3	2	2
6	DWARF-SHRUB MIRE	72 ⁴	59 ⁵	8 ³	13 ⁴	105 ⁴	103 ⁴	26 ⁴	30 ⁴					4	4	
20	TALL-HERB MEADOW	72 ⁵	19 ²	17 ⁵	15 ⁵	>1600 ¹⁰	505 ⁹	80 ¹⁰	65 ⁹	>1600 ⁷	>1600 ⁷	97 ⁷	79 ⁷	5	9	7
21	FERN-HERB MEADOW	86 ⁶	42 ⁴	25 ⁶	22 ⁶	>1600 ¹¹	>1600 ¹¹	72 ⁹	67 ¹⁰					6	11	
18	MYRTILLUS MEADOW	119 ⁷	131 ⁷	41 ¹⁰	39 ⁷	164 ⁵	186 ⁶	46 ⁶	49 ⁶	245 ²	571 ⁴	53 ²	63 ⁴	7	5	3
26	DRYAS HEATH	125 ⁸	159 ⁹	37 ⁸	45 ⁸	167 ⁶	203 ⁷	42 ⁵	50 ⁷	>1600 ⁶	>1600 ⁶	94 ⁵	72 ⁶	8	7	6
27	DWARF-SHRUB HEATH (1200m)	137 ⁹	148 ⁸	37 ⁹	45 ⁹	200 ⁷	138 ⁵	50 ⁷	45 ⁵					9	6	
23	LOW-HERB MEADOW	200 ¹⁰	192 ¹⁰	32 ⁷	48 ¹⁰	403 ⁸	515 ¹⁰	81 ¹¹	70 ¹¹	>1600 ⁵	>1600 ⁵	95 ⁶	70 ⁵	10	10	5
29	GRASS HEATH (1200 m)	330 ¹¹	348 ¹¹	59 ¹¹	55 ¹¹	578 ⁹	228 ⁸	67 ⁸	55 ⁸					11	8	

III. . VEGETATION ZONATION ON TRACKS THROUGH DWARF SHRUB HEATHS
IN THE TORNETRÄSK AREA, NORTHERN SWEDEN

VEGETATION ZONATION ON TRACKS THROUGH DWARF SHRUB HEATHS IN THE TORNETRÄSK AREA, NORTHERN SWEDEN.

ABSTRACT

Tracks passing through Empetrum hermaphroditum-dominated dwarf-shrub heaths were studied in the Torneträsk area in northern Sweden.

In used tracks (around 2000 passages) on flat ground without obstacles a narrow vegetation-free zone in the middle of the track is evident, bordered by a zone dominated by small cryptogams, which in turn is bordered by a zone with cryptogams and grasses (Festuca ovina, Deschampsia flexuosa or Calamagrostis lapponica). Approximately 2-3 dm from the middle of the track Vaccinium vitis-idaea and V. myrtillus are dominant, but outside this zone Empetrum hermaphroditum and V. uliginosum successively appear.

When trampling ceases, grasses will invade the center of the track in about one year, very soon followed by Vaccinium myrtillus and V. vitis-idaea. Empetrum hermaphroditum takes much longer to recover, probably as a result of its lack of rhizomes. It seems that narrow tracks need some decades to recover totally, but it is also clear that wider tracks need much longer periods for regeneration.

1 INTRODUCTION

Tracks in the landscape are not only the results of human trampling. Impacts on the vegetation caused by trampling have probably occurred for millions of years. For example, Kurtén (1971) has shown that aggregation of mammals into herds occurred at least 48,000,000 years ago, and probably earlier. Many species of animals move regularly along the same routes, thus concentrating their trampling impact upon the vegetation. Variations in the time of movement and the way in which the animals move, produce variations in the vegetation associated with the tracks. For example, some animals use a track for only a short period of the year, whereas others move along the same track throughout the whole year.

In Lapland it is probable that many tracks were commonly used by both man and animals in earlier times (Andersson, 1977). These tracks were probably created initially by animals. Reindeer used the same routes from year to year and thereby created tracks. Some of these tracks were never used by man.

Tracks offer a very special environment to those plants which can survive there: trampling is a strong selective force for track plants. The intensity of trampling is different in the middle of tracks to that at the sides and is probably associated with a corresponding zonation of the track vegetation. Such zonation will probably only occur if a track has been used constantly for a long time during which a balance has been established between the presence of various plant species and the degree of trampling.

Studies on trampled vegetation have been made since the 1930's. In a classical study by Bates (1935), vegetation descriptions were made of paths, side-walks, dirt tracks and gateways. The vegetation types were, however, those of temperate regions found in England. During the 1960's and 1970's many studies of trampling were published in the ecological literature (reviews by Liddle, 1975a; Satchell & Marren, 1976; Liljelund et al., 1977). Thus, trampling in many types of vegetation has been described, but the studies have mainly been concentrated on the early stages of trampling and its effects on the vegetation. Also, many studies have described the regeneration of vegetation in tracks, but fewer investigations have been made of the vegetation in the constantly used tracks, where there is a balance between the vegetation and the degree of trampling. Indeed, it is very difficult to develop a methodology for relating the type of vegetation on the track to an exact degree of trampling. Bayfield (1971) made an attempt, however, and was able to demonstrate trampling effects outside the visible edges of the tracks. In some cases, two small tracks may lie parallel to each other and may easily be mistaken for one track.

The present investigation is part of a larger project into the relationships between trampling and vegetation in alpine and

sub-alpine ecosystems in the Torneträsk area (Fig. 1). As the most common sub-alpine and alpine vegetation type of northern Sweden is the one dominated by *Empetrum hermaphroditum* (Vegetationskartor, 1977-84), this paper concentrates on this type of vegetation. Earlier work has shown that there are zonations associated with tracks passing through heath vegetation types in Scotland (Bayfield, 1981). Those vegetation types are similar to the *Empetrum* vegetation found in the Torneträsk area. Zonations have also been described in other vegetation types, such as those of sandy areas (Liddle & Grieg-Smith, 1975).

Various methods have been used to detect the vegetation zones around tracks, such as estimates of frequency, cover and biomass. Liddle & Grieg-Smith (1975) also tried to define the vegetation zones around the tracks mathematically. Other studies have concerned vegetation zones resulting from trampling around holiday huts in northern Finland (Hoogesteger, 1976) and from military training areas (Ingelög et al., 1977).

In general, it can be postulated that vegetation types similar to the *Empetrum* heath, where stems grow prostrate on the ground surface (e.g. *Empetrum nigrum*, *E. hermaphroditum* and *Calluna vulgaris*), are those which are the most vulnerable to trampling and will, therefore, be found farthest from the centre of the track (Kellomäki, 1977; Hoogesteger, 1976; Harrison, 1981). Rhizomatous species and some species of mosses and lichens are less susceptible to trampling, although some species of *Cladonia* are known to be sensitive (Bayfield et al., 1981).

It is difficult to determine the causes of the zonation of tracks. Bates (1935) emphasized the importance of the growth form, while Hylgaard (1980) stressed the importance of the reproductive structures of plants in determining their presence in the vegetation zones. Many authors have attempted to relate the vegetation zonation of tracks to various degrees and methods of trampling: Satchell & Marren (1976) reviewed the range of methods in use. One method employs very thin metal rods buried in the track to measure the degree of tramp-

ling across a transect of the track (Bayfield, 1971). Finally, some investigators, e.g. Bayfield (1981), have enclosed parts of used tracks to study the process of regeneration. This practice has also been introduced to stimulate the regeneration of used tracks in order to make them less vulnerable to continued trampling.

It would be expected that there is a zonation of plant species within the tracks through the Empetrum vegetation of northern Sweden as a result of varying degrees of trampling. This paper discusses some of the problems associated with such a possible zonation. These problems can be expressed as the three following questions:

1. Is there a zonation of the vegetation of tracks through Empetrum heaths and, if so, how can the zones be described?
2. What are the ecological reasons behind such zonation?
3. If the trampling ceases on a track through Empetrum -dominated vegetation, what changes will occur in the vegetation on and surrounding the track?

2 METHODS

2.1 Choice of experimental tracks

Studies were undertaken in areas close to Abisko Scientific Research Station (Fig 1). Three experimental tracks were investigated in open mountain birch vegetation (Betula pubescens f. tortuosa) where the ground layer consisted mainly of Empetrum and Vaccinium myrtillus. This vegetation was classified as Empetrum-Vaccinium myrtillus type and Empetrum type according to Sonesson & Lundberg (1974). Some degree of variation occurred in the sites studied, depending upon the water conditions and the amount of snow in the winter. See further Mårtensson (1956), Sonesson (1967, 1970 and 1974) for general information about the investigation area.

Nomenclature for cryptogams is according to Krok & Almquist (1962), for vascular plants to Lid (1974) and for mammals to van den Brink (1958).

In order to assess the earlier use of the experimental tracks, measurements were made of parts of the track which were still in use in 1978-80 during the experimental period. Noticeboards were erected at the ends of the tracks and users were asked to record each occasion on which they used the track. Independent observations, using binoculars, showed that the results of the census were within 30% of the actual usage.

2.1.1 Experimental track (A)

This track was situated in Empetrum-Vaccinium myrtillus type vegetation which can be considered as a mesic heath (Sonesson & Lundberg, 1974). The track was situated 400 m above sea level and might have existed already in 1912. During the last 30 years, the frequency of use has probably remained constant. Observations from 1978-80 showed that the equivalent of 1000 people passed along this track each year during the growing season. During winter, the snow cover on the track was normal for the region, i.e. about 50 cm in February.

2.1.2 Experimental track (B)

This track is part of the track described above but this section was located in Empetrum-type dry heath vegetation where the winter snow cover was only sparse, e.g. 20 cm in February 1981, while some patches were snow-free.

2.1.3 Experimental track (C)

This track was located in Empetrum-Vaccinium myrtillus type mesic heath vegetation. Winter snow cover here was considerable, e.g. 50 to 80 cm in February, 1981. The track was situated

in dense birch forest at an altitude of 400 to 420 m above sea level. This track differs from that described above in that it was formed recently (1974). Observations during 1978-80 showed that the equivalent of 2000 people used the track each year during the growing season on sections which were not closed as part of the experiment. During the years 1974 to 1977, prior to the experimental period, it was assumed that the equivalent of between 500 and 1000 people used the track during the growing season.

2.2 Experimental design (Fig. 2).

In the autumn of 1977, enclosures were established on the experimental tracks to prevent trampling. Within these enclosures, a number of transects were established so that vegetation change could be monitored during the process of revegetation (see further section 2.3 below). New tracks were formed outside the enclosures and information boards were placed at the start of the tracks in order to explain the experiments to the public. Consequently, by the beginning of the growing season of 1978, some of the tracks had not been trampled for about 6 months, during which there had been little plant growth. The transects were, therefore, established in early June 1978 and the first observations were registered. Further observations were made in July 1978, and then during the same month in following years.

2.3 Criteria for selecting the transects

The following conditions were required before a transect was established on the tracks:

- i) The site of the transect had to be flat and without obstacles such as trees or boulders.
- ii) The width of the track had to be the same at each transect.

These conditions were satisfied at 16 locations on track (A),

8 on track (B) and 13 on track (C). From these possibilities, 4 locations per track were selected randomly and in these places the transects were established.

2.4 Investigation in the transects and their presentation

The transects were of rectangular form, 100 x 50 cm, and they were sub-divided into 200 plots each of 25 cm² (Fig. 2). On each sampling occasion, the presence or absence of each plant species was recorded in each plot. These data could be presented as the frequency of each species in rows, each row comprising 10 plots, which were parallel to the track (Fig. 2). The rows thus represented a complete cross-section of the track from one periphery, through the central region, to the other periphery.

The presence or absence measured across the transects for each species in all the 12 transects were synthesized into 200 diagrammes. However, not all of these transect diagrammes are presented here, and those which are included, possess only 19 rows rather than the 20, because there were some minor errors in the location of sampling frames from year to year. This error has been minimized to some extent by omitting one row from the analyses.

The vegetation descriptions were derived from all of the 200 diagrammes, and Figs. 6, and 10-13 illustrate the major trends found in the data. Figures 3-5 present the mean values for all the grass species, Vaccinium myrtillus, V. vitis-idaea and Empetrum hermaphroditum determined from the three tracks. The principle vegetation zones of the tracks were derived from all of the data and are presented in Figs. 7 and 8. However, Fig. 8 also includes material collected from other tracks (see section 2.5 below).

2.5 Transects across older tracks

In addition to the three tracks described above, 11 others

were also investigated. These tracks had been abandoned either recently or at some time in the past for a variety of reasons. All were located in the western part of Torne Lappmark, mostly in the Torneträsk area (Table 2) and all passed through vegetation dominated by Empetrum hermaphroditum. In most cases, the year when trampling ceased could be determined.

The most common method of determining when trampling ceased was by studying birch trees which had fallen across the tracks. When this happens, that part of the track is obstructed, and an alternative route is created and the trampling of the original portion of the track ceases. As the fallen birch tree usually produces new shoots, which can be age-determined by counting the annual rings, the year in which the tree had fallen can be determined. A transect across a broad, old track is presented in Fig. 15, and some data on this track, are given in Table 2 (Abisko).

Finally, a quite different track was observed in the Kilpisjärvi National Park, northern Finland.

In this national park there are strict regulations to prevent visitors from leaving authorized tracks and it may, therefore, be assumed that additional trampling by people is minimal. At the end of World War II, however, German troops who occupied northern Finland, excavated several fortifications in the national park, linking them by means of an earth-road. Since 1945, when the Germans left the area, the national park regulations have been observed and the road has not been used. Thus, no trampling now occurs on the track, which partly passes through Empetrum hermaphroditum-dominated vegetation.

3. RESULTS

3.1 Currently trampled tracks.

The sensitivity of trampling on tracks (A) and (B) was obvious as the peat and organic soil were eroded away in the middle of them, although the mineral soil was not eroded. However, the peat soil was not missing from the middle of track (C), which was covered by peaty material. Excavations of tracks (A), (B)

and (C) showed the presence of living rhizomes of Vaccinium vitis-idaea and V. myrtillus in track (C) only. Calamagrostis lapponica only occurred around track (C) but its rhizomes were absent in the peaty soil of the track itself.

In general, there was a thin zone of 5 to 10 cm in the middle of all three tracks, where vegetation was totally absent. This zone was wider on track (C) than on the others, but was too thin to be detected by the sampling system used in this study (Figs. 3-5). It was, however, evident in more than 50% of the transects recorded in June, 1978.

Apart from the vegetation-free zones of the tracks, it was possible in some places but difficult in others to detect definable "vegetation types", which showed a zonation parallel to the tracks. It appeared that the tracks were vegetated by a number of vegetation types which, in some parts of the track, showed a zonation parallel to the track (cf. Fig. 9).

The three tracks appeared to have similar zones, defined by the most common plant species (Figs. 3-5). This has enabled data from the three transects to be regarded as replicates and means can be presented. Some minor differences occurred, however, between the transects. For example, Vaccinium myrtillus was sparse in track (B), whereas Empetrum occurred farther from the middle of the track in track (C) than in the others. Also, track (C) showed a greater abundance of Vaccinium myrtillus and the grasses.

3.2 Successional stages in the re-vegetation of the tracks (Table 1.).

The twelve transects were also used to study the vegetation during the years 1979 and 1980. The most obvious frequency changes in the distribution of the most common plants were:

Empetrum hermaphroditum advanced 5-15 cm from the edges to the middle of the track over the observation period but its frequency on the track was low.

Vaccinium myrtillus recolonized the whole track within only one year, but three years were required before it attained the frequency found outside the track.

Vaccinium vitis-idaea recolonized the whole track in three years, but it did not attain the frequency found outside the track within this period.

Vaccinium uliginosum experienced extreme difficulty in recolonizing the track and even decreased in frequency at the edges of the track after trampling had ceased.

Grasses included Festuca ovina, Calamagrostis lapponica and Deschampsia flexuosa. One year after trampling had ceased, these grasses had recolonized the whole track but after a further two years, the frequencies at the edges of the track began to decrease.

The only other vascular plant species was birch. This species was able to colonize abandoned tracks within a three-year period. It colonized the middle of the track and could be common on some sections of the track already one year after trampling had ceased.

Cryptogams showed a greater diversity of recolonizing than vascular plants. It was, therefore, less meaningful to summarize the cryptogam data in diagrammatic form. Some processes of cryptogam recolonization can, however, be described where they were similar between transects, but there was still great variation with time. Examples of this situation were found for Dicranaceae and some species of Cladonia (Fig. 6), which recolonized the edges of the tracks initially but then disappeared after 2-5 years while colonizing the centre of the tracks. A similar, but less pronounced, type of recolonization was shown by some Polytrichaceae. A different type of colonization was shown by Pohlia nutans and some Hepaticae which initially colonized the middle of the track but from which they disappeared after two years: these species were not found to colonize the edges of the tracks (Fig. 15). Species of Peltigera, Nephroma arcticum and Cetraria islandica

grew into the track from the areas surrounding it in a similar way to *Empetrum hermaphroditum* and *Vaccinium uliginosum*. However, the lichen species rarely reached the middle of the track within three years (Fig. 14).

3.3 Old tracks in north-west Torne lappmark (Table 2.)

These tracks had been in disuse for various periods of time but even those in disuse for the longest period had not been completely recolonized by vascular plants. In the somewhat different track observed in the Kilipsjärvi National Park of northern Finland in the autumn of 1979 only 10% of the road was covered by phanerogams. However, 90% of the 6 m wide road was covered by cryptogams where nearly all of the species common in the areas surrounding the road were represented on it. The recolonization of the old military road has taken place in two ways. Firstly, plants have recolonized by vegetative spread from the borders of the road. This process was slow and only 0.5 m of the edges of the road had been recolonized. Secondly, the phanerogams colonized the road from seeds. Age determinations of some of these species showed that the period of recolonization was between 1945 and 1947. The diameters of clones of *Empetrum hermaphroditum* and *Vaccinium uliginosum*, which had been initiated from seeds, were 25 and 30 cm respectively.

4 DISCUSSION

4.1 Methods

4.1.1 The selection of transects across the tracks and trampling impact

Theoretically, tracks should be more worn in the middle than at the sides. Such tracks can be found in areas which are more or less free from trees and larger stones. If, however, the trampling occurs in a dense forest there will be an abrupt change from the untrampled to trampled areas.

The tracks studied in the present paper, pass through terrain which is flat in some areas yet has large boulders in others. The amount of shrubs and trees also varies, thus giving the track considerable differences in appearance. In some places it is narrow and passes between trees and large boulders, whereas in others it is broader and shows clear vegetation zones. These zones, which result from various intensities of trampling, may be wide or thin. It is, therefore, difficult to compare different transects that are laid out in a totally random manner along a track. This explains why it was only possible to use partly selected transects in the present investigation.

As the vegetation surrounding the experimental tracks upon which the transects were located clearly can be classified as either *Empetrum-Myrtillus* type or *Empetrum* type (cf. Sonesson & Lundberg 1974), one can assume that a proposed zonation around those tracks may broadly be general for at least *Empetrum*-dominated vegetation of the Torneträsk area. It should be noted that the proposed principle zonation in section 4.2 is only relevant when discussing parts of tracks without large obstacles such as trees or boulders. Such parts are excluded before the twelve transects were randomly placed along the tracks.

4.1.2 The sampling method

Frequency is the variable which has been chosen to describe the vegetation on the transects of the tracks. Pilot studies showed that cover was not a suitable variable to measure. In order to measure cover, small sample squares were required to identify the narrow zones of vegetation and this resulted in a requirement for an impossibly large number of sample squares. Frequency was a practical possibility, because fewer squares were required. Another advantage of using frequency as a variable was that many different people could record data in the same way, whereas estimates of cover are susceptible to personal bias.

The identification of mosses and lichens was often difficult as these plants were often in the juvenile phase and removing them for observation under the microscope would have destroyed the permanent transect sample areas. It was therefore, necessary to classify these species into groups such as Dicranum species (spp) etc. The description of the vegetation zones of the track have not been based on the cryptogam data mainly because of the difficulty in identifying the cryptogams to species.

4.1.3 The relevance of old disused tracks in the present context

The old disused tracks had been used to construct a picture of the vegetation succession taking place in abandoned tracks passing through Empetrum vegetation. Although this may not be satisfactory from a statistical point of view, the use of the old tracks was the only way in the present investigation to reconstruct the revegetation of tracks which have been disused for more than three years. The figures relating to those disused for 10 and 20 years are more uncertain than those relating to tracks disused for shorter periods (Fig. 8).

The difficulty with which wide tracks are revegetated is

illustrated by the one depicted in Fig. 15, which has been disused for a long time yet is revegetated less than a narrower track (Nakerjaure) described in Table 2. It seems, therefore, that the revegetation varies according to the width, and wide tracks present a particularly difficult obstacle to vegetatively reproducing species. The military road in the Kilpisjärvi region of northern Finland, described above, is a particularly good example of this.

The trampling over wide areas surrounding holiday huts in northern Finland and in the Torneträsk areas is related to the trampling of broad tracks (Hoogesteger 1976). These broad areas of trampling correspond, to some extent, to the zones described in this paper.

4.1.4 Variation between transects

Large variations in vegetation development between transects are evident. All of the species found on one particular transect are presented in Fig. 6 but there is insufficient space to present a species list for each of the 12 transects studied. Unfortunately, the presentation of mean values for the zones confuses the results and vegetation zones become more difficult to identify. This is particularly true for the distributions of the cryptogams. The main reason for this is probably that the speed of the successions varies greatly along the track after it has fallen into disuse. Fig. 3-5 thus obscures many of the detailed results and it is essential to consider such complete results as presented in Fig. 6.

4.2 Vegetation zones on tracks passing through Empetrum vegetation

Although there is often a great variation in the zonation along separate parts of the tracks (cf. an example in Fig.9) as well as between different tracks, the same zones are usually discernible according to the data of all transects investiga-

ted and with special reference to the vascular plants;

- (1) Earth zone: phanerogams and cryptogams are absent
- (2) Earth-cryptogam zone: only cryptogams are present
- (3) Grass-cryptogam zone: among the phanerogams, grasses (Calamagrostis lapponica, Festuca ovina or Deschampsia flexuosa) are very dominating in this zone. Dwarf shrubs are absent.
- (4) Grass-Vaccinium zone: Vaccinium myrtillus and V. vitis-idaea are the two dominating phanerogams in this zone. Grasses are still more abundant than in zones 5 and 6.
- (5) Empetrum-Vaccinium zone: Empetrum hermaphroditum is present in this zone, but the species is somewhat less abundant here than in zone 6. Vaccinium myrtillus and V. vitis-idaea are more common here than in zone 6.
- (6) Virgin zone: Vaccinium uliginosum is present in this zone.
This species is more or less absent in zone 5.

This principle zonation is shown in Fig. 7. The cryptogams are usually distributed as follows:

- (1) Earth zone: permanent cryptogam cover is absent
- (2) Earth-cryptogam zone: very small lichens, e.g. juveniles of Cladonia sp. and mosses such as Dicranum sp, Polytrichum sp. and Pholia nutans are found.
- (3) Grass-cryptogam zone: Polytrichum species, Dicranum species and Cladonia species occur here.
- (4) Grass-Vaccinium zone: This is similar to zone 3 but Nephroma arcticum and species of Cetraria, and Peltigera species also occur but at low frequencies.
- (5) Empetrum-Vaccinium zone: This is similar to zone 4 but higher frequencies of Nephroma arcticum and species of Cetraria, and Peltigera occur.
- (6) Virgin vegetation zone: Here, the cryptogam community is similar to that of zone 5.

Only two of the vascular cryptogams of the area were sufficiently represented on the tracks to require consideration.

Equisetum arvense and E. scirpoides are quite resistant to trampling and are often found in the grass-cryptogam zone. They are also abundant in the grass-Vaccinium zone but are infrequent in the virgin vegetation zone.

Of the phanerogams, two species additional to those characterizing the zones merit consideration in relation to trampling. Andromeda polifolia reacts to trampling in a similar way to Empetrum, i.e. it is sensitive to trampling. Arctostaphylos alpina is sensitive to trampling and, like Vaccinium uliginosum, is only found in the virgin vegetation zone furthest away from the middle of the track.

How can the association of the various species with particular zones be explained?

Zone 1: The earth zone

Earlier investigations show that many small mosses and grasses are resistant to trampling (Lidell, 1975; Satchell and Moran, 1976). In Zone 1, the earth zone of the present study, the few moss and lichen species occurring are probably poorly adapted to trampling, but are present, because they can colonize ground very quickly. It should be remembered that the tracks are disused for about one month during a period when the mosses and lichens were not covered by snow. This month therefore, provides the opportunity for colonization. The species of this zone may be regarded as opportunistic colonizers which are sensitive to trampling but can quickly recolonize when trampling ceases.

Zone 2: The earth-cryptogam zone

This is also a zone in which colonization occurs quickly.

Zone 3: The grass-cryptogam zone

In this zone there are great variations between tracks. Of the phanerogams, one species has always been dominant but this species varied from track to track. However, there is always a zone of grass between the earth and cryptogam-dominated track centre and the edges where various dwarf shrubs begin to colonize. It is interesting to note that even if the three grass

species recorded here are found in this small zone, their mechanisms of spread are different. Calamagrostis lapponica spreads mainly by rhizomes from the areas surrounding the tracks while Festuca ovina and Deschampsia flexuosa mostly spread by seed and then form small clones on the tracks.

Zone 4: The grass-Vaccinium zone

Two rhizomatous dwarf shrubs, Vaccinium vitis-idaea and V. myrtillus, occur in Zone 4. Excavations of Zone 4 in the three tracks showed that living rhizomes were present in each of the three tracks and living rhizomes, particularly those of V. vitis-idaea, were even present under the middle, or earth zone, of track (G). The rhizomatous spread of these species must explain their ability to quickly recolonize the lesser trampled sides of the track, and to survive under heavier trampling.

Zone 5: Empetrum-Vaccinium zone

Empetrum hermaphroditum begins to occur in this zone and a balance appears to exist between recolonization and death of shoots. There are also traces of V. uliginosum in this zone, but this species seems to be very sensitive to trampling and even if some rhizomes were found they would be so shallow in the soil that trampling would probably affect them. Thus, there is no effective recolonization by V. uliginosum in this zone.

Zone 6: Virgin vegetation zone

Vaccinium uliginosum occurs in its normal habitat in this zone and appears to be the most sensitive phanerogam in relation to trampling.

Already in 1908 Warming pointed out that Empetrum hermaphroditum (then called E. nigrum) was a species which grew from above-ground shoots rather than rhizomes.

The growing points of this species are, therefore, susceptible to trampling which explains why Empetrum is affected more by trampling than Vaccinium vitis-idaea and V. myrtillus, which are rhizomatous.

The difference between Zone 4, the grass-Vaccinium zone, and Zone 5, the Empetrum-Vaccinium zone, is clearly visible as Empetrum obviously dominates Zone 5. However, this negatively affects many of the cryptogams which are the earliest colonizers of the middle of the track, as they are not found in Zones 5 and 6, probably as a result of competition.

Many workers such as Holmström (1970), Hoogesteger (1976), Ingelög et al. (1977), Bayfield (1979) and Sternlock & Dean (1979) have studied trampling effects on plants from vegetation types similar to those investigated here. Hoogesteger (1976) found similar responses of the plants to trampling as those described here with the exception of Vaccinium uliginosum. This species, she suggests, reacted to trampling in a similar way as V. vitis-idaea and V. myrtillus, whereas in this paper, V. uliginosum was found to be much more sensitive to trampling than the other two species. Sternlock & Dean (1979) also suggested, like Hoogesteger (1976), that V. uliginosum is not sensitive to trampling. Another difference between the work of Hoogesteger (1976) and the present work is that she describes the Cladonia species as a group sensitive to trampling, whereas they were found here in a heavily trampled zone. This difference may reflect the drier nature of Hoogesteger's site, where Cladonia species will be more dominant. In this case, they may be more sensitive to trampling when growing in pure stands than when growing together with other species, as at the present investigation site. Bayfield (1982) found large variations in the sensitivity to trampling of different Cladonia species and Kellomäki (1977) regarded the cryptogams as a group sensitive to trampling in general, although he based his assessment on the biomass of cryptogams in different types of previously untrampled vegetation. It may be assumed, therefore, that many cryptogams, such as mosses and lichens, are sensitive to trampling in areas which have been previously undisturbed, whereas they are the group of species best able to recolonize and withstand trampling on established tracks.

In relation to the phanerogams, Ingelög et al. (1977) points out that Vaccinium vitis-idaea and V. myrtillus are vulne-

rable to mechanical impact. However, the vulnerability of V. myrtillus to mechanical impact results, perhaps, from the comparison these authors made of this species with Deschampsia flexuosa and other grasses and herbs. Also, the mechanical impact experienced in their plots was more from vehicles than from human trampling. This may also explain why V. myrtillus was considered to be sensitive in that investigation.

4.3 Vegetation successions on tracks

Most of the dominant species of the Empetrum vegetation studied are clonal plants and their ability to grow vegetatively should, therefore, be of particular importance in the recolonization of the tracks. Assuming this ability as the main cause of the revegetation, the following description may be made.

- (a) Initially, the bare soil is colonized by mosses and lichens through the spread of spores and, to some extent, by fragmentation of the thallus resulting from trampling. Some of the species which are spread by spores, e.g. Parmelia species and Pohlia nutans, disappear after only a few years when the competition from other species increases. There are, however, examples where Pohlia nutans has remained for 5 years but these are associated with tracks which are very broad and on which, consequently, complete revegetation by the clonal dwarf shrubs takes a particularly long time.
- (b) Grasses which occur initially take longer to invade the middle of the track than mosses and lichens. The mechanisms whereby the middle is invaded vary from species to species. Calamagrostis lapponica spreads by rhizome growth whereas other species such as Festuca ovina and Deschampsia flexuosa initially colonize from seedlings although some vegetative colonization is possible. As no living rhizomes of Calamagrostis lapponica have been found immediately after trampling has ceased, it may be assumed that recolonization occurs from the growth into the track of rhizomes from vegetation along the edges.

This contrasts with the recolonization by Vaccinium vitis-idaea as the rhizomes of this species may survive trampling under the track and new shoots may be produced from these old rhizomes. It commonly occurs that the grasses diminish in frequency after some years when the dwarf shrubs Empetrum hermaphroditum, Vaccinium vitis-idaea and V. myrtillus become abundant in the middle of the track.

- (c) Vaccinium vitis-idaea and V. myrtillus show very similar ways of recolonization. They both appear sporadically, even in the middle of the track, after only a few years. Although living rhizomes were only found in track (C) during its period of usage, there were no great differences between tracks (A), (B) and (C). As no living rhizomes of the two Vaccinium species were found in tracks (A) and (B) during their usage, it seems possible that rhizomes grew 20 to 30 cm in just a few years to recolonize the track (Figs. 3-5). However, the two Vaccinium species do not colonize as extensively as Empetrum hermaphroditum.
- (d) Empetrum hermaphroditum and Vaccinium uliginosum appear late during the revegetation. Empetrum hermaphroditum is totally dependent upon the growth of above-ground shoots for recolonization and roots are produced from these shoots after about 12 years. Vaccinium uliginosum also recolonizes by the growth of above ground shoots but also has some ability to grow from rhizomes. It would be expected, therefore, that V. uliginosum should recolonize faster than E. hermaphroditum but this does not seem to occur here as V. uliginosum is the last phanerogam of importance to recolonize. The current year's shoots of Empetrum hermaphroditum can, to some extent, be compared with rhizomes as they can grow up to 6 cm each year. This may explain why it recolonizes faster than Vaccinium uliginosum. In many places, however, Empetrum retreats after periods of fast vegetative recolonization and the shoots die. Also, heavy grazing has occurred on some tracks where Empetrum has grown quickly. It appears that the combination of grazing and some abiotic

factors such as frost can prevent Empetrum from quickly recolonizing. It should be remembered that grazing by rodents has been shown to be very important in this type of vegetation (Eriksson, 1977; Emanuelsson, 1980, 1984b). This process of rodent grazing may interfere to a great extent in the recolonization. Therefore, if a track is abandoned during a period of intense grazing, revegetation will differ from that occurring after an ungrazed track has fallen into disuse.

- (e) Finally, there is a group of species with an erratic method of colonization; i.e. mainly lichens of the genera Nephroma and Peltigera. The pattern of recolonization by this group varies from track to track. However, the most common pattern is for late recolonization - even later than Vaccinium uliginosum but on some tracks they are early colonizers (Fig. 6). In the latter case, early recolonization takes place from fragments of lichen surviving after large plants have been trampled and destroyed. These fragments can lead to rapid recolonization even in the middle of a track. To some extent, the process of fragmentation may represent experimental error. In order to stop trampling on an existing track, a new track nearby had to be made and it is possible that fragments of trampled lichens from the new track contaminated the experimental track.

4.4 The time required for revegetation of disused tracks.

How long does it take, then, for the revegetation of a track passing through Empetrum vegetation. Typical tracks, about 30 cm wide during use, show very slight traces of trampling 40 to 60 years after trampling has ceased. After only 10 years of disuse, a track may appear superficially to have recovered while the cover of the phanerogams can attain 60% after 3 years. However, the speed of recolonization can be reduced by a number of factors.

- (a) The age of the track when it begins to recover can greatly

affect the speed of recovery. Thus the speed of recovery decreases as the age of the track increases. This may be the result of the total destruction of the peat or organic layer of the soil of old tracks. The organic layer protects those rhizomes which survive trampling and these rhizomes may enable fast recolonization as in the case of Vaccinium myrtillus.

- (b) Tracks which pass through dry Empetrum heaths recover more slowly than those passing through wetter Empetrum heaths.
- (c) The width of the track also seems to be important in determining the speed of recolonization by species such as Empetrum hermaphroditum and Vaccinium uliginosum.
- (d) Many of the tracks are used by animals as well as humans and the experimental closure of the track has only stopped the trampling by humans. New shoots appearing on disused tracks are often grazed by small rodents and hares, as was observed several times during the investigation. A similar example in more temperate areas is the intense grazing by rabbits along tracks used by people passing through Calluna vegetation. This has been demonstrated, for example, by Svensson (1984) from the Sandhammaren area of Scania, southern Sweden.

The revegetation of a track passing through Empetrum vegetation is, therefore, easiest if the track was created fairly recently, is narrow and is located on fairly wet vegetation. The revegetation of larger areas of such vegetation will be much more difficult than that of narrow strips, and thus the results of this study cannot be used to predict the stages or speed of revegetation of such large areas.

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5. REFERENCES

- Andersson, H. 1977. Taiga och Tundra. - Stockholm.
- Bates, G.H. 1935. The vegetation of footpaths, sidewalks, cart-tracks and gateways. *J.Ecol.* 25 469-81.
- Bayfield, N.G. 1971. Some effects of walking and skiing on vegetation at Cairngorm. In: *The Scientific Management of Animal and Plant Communities for Conservation* (Ed. E. Duffey and A.S Watt), pp. 469-85. Blackwell Scientific Publications, Oxford.
- Bayfield, N. 1979. Recovery of four montane heath communities on Cairngorm, Scotland, from disturbance by trampling. *Biol. Conserv.*, 15:165-79.
- Bayfield, N.G., Urquhart, U.H. and Cooper, S.M. 1981. Susceptibility of four species of *Cladonia* to disturbance by trampling in the Cairngorm mountains, Scotland. *J. Appl. Ecol.* 18:303-310.
- Bayfield, N.G. 1982. Experimental closure of footpaths in a woodland national nature reserve in Scotland. *Biol. Conserv.* 22:229-237.
- van den Brink, F.H. 1958. Alla Europas däggdjur. - Stockholm.
- Emanuelsson, U. 1980. Den ekologiska betydelsen av mekanisk påverkan på vegetationen i fjällterräng. *Fauna och Flora* 75:1.
- Emanuelsson, U. 1984a. Short-term effects of trampling on subalpine and alpine vegetation in Torne lappmark, Northern

- Sweden. Dept. of Plant Ecology, Univ. of Lund (In manuscript).
- Emanuelsson, U. 1984b. Dynamics of dwarf shrub heaths in relation to grazing of small rodents in the Torneträsk area, northern Sweden. - Dept. of Plant Ecology, Univ. of Lund (In manuscript).
- Ericson, L. 1977. The influence of voles and lemmings on the vegetation in a coniferous forest during a 4-year period in northern Sweden. *Wahlenbergia*, vol. 4.
- Harrison, C. 1981. Recovery of lowland grassland and heathland in southern England from disturbance by seasonal trampling. *Biol. Conserv.* 19:119-130.
- Holmström, H. 1970 Undersökning av vegetationens slitagetålighet på fritidsområden i södra Finland. Helsingfors regionplaneförbund. (Mimeo.).
- Hoogesteger, M. 1976. Changes in vegetation around the refuge huts in Koilliskaira forest area. *Silva Fennica*, Vol 10, No.1:40-53.
- Hylgaard, T. 1980. Recovery of plant communities on coastal sand-dunes disturbed by human trampling. *Biol. Conserv.* 19:15-25.
- Ingelög, T., Olsson, M.T. & Bödvarsson, H. 1977. Effekter av långvarigt tramp och fordonskörning på mark, vegetation och vissa markdjur i ett äldre tallbestånd.-Avd. för skogsekologi och skoglig marklära, Skogshögskolan. Rapporter och uppsatser nr 27.
- Kellomäki, S. 1977. Deterioration of forest ground cover during trampling. -*Silva Fennica* 11 153-61.
- Krok, T.O.B.N. & Almquist, S. 1962. *Svensk flora för skolor. Kryptogamer*. 25 uppl. - Stockholm.
- Kurten, B. 1971. *The age of mammals*. - London.
- Lid, J. 1974. *Norsk og svensk flora*. 2 uppl. - Oslo.
- Liddle, M.J. 1975a. A selective review of the ecological effects of human trampling on natural ecosystems. -*Biol. Conserv.* 7:17-36.
- Liddle, M.J. 1975b. A theoretical relationship between the primary productivity of vegetation and its ability to tolerate trampling. *Biol Conserv.* 8:251-255.

- Liddle, M.J. and Greig-Smith, P. 1975. A survey of tracks and paths in a sand dune ecosystem. II. Vegetation. J. Appl. Ecol. 12:909-930.
- Liljelund, L-E., Emanuelsson, U., Florgård, C. and Hofman-Bang, V. 1977. Kunskapsöversikt och forskningsbehov rörande mekanisk påverkan på mark och vegetation. Meddelande Nr 79/4 från Botaniska Institutionen vid Stockholms Universitet (Mimeo.).
- Mårtensson, O. 1956. Bryophytes of the Torneträsk area, northern Swedish Lapland. LLL. General part. - K. Sv. Vet. Akad. Avhandl. i Naturskyddsärenden 15, 94 pp.
- Satchell, J.E. and Marren, P.R. 1976. The effects of recreation on the ecology of natural landscapes. Nature and Environment series No.11 Council of Europe.
- Sonesson, M. 1967. Studies on mire vegetation in the Torneträsk area, northern Sweden. I. Regional aspects. - Botaniska Notiser 120:272-296.
- Sonesson, M. 1970. Studies on mire vegetation in the Torneträsk area, Northern Sweden. III. Communities of the poor mires. - Opera Botanica 26:120 pp.
- Sonesson, M. 1974. Late Quarternary forest development of the Torneträsk area, North Sweden. 2. Pollen analytical evidence. - Oikos 25:288-307.
- Sonesson, M. 1980. Klimatet och skogsgränsen i Abisko. - Fauna och Flora Årg 75:1.
- Sonesson, M. & Lundberg, B. 1974. Late Quaternary forest development of the Torneträsk area, North Sweden. I. Structure of modern forest ecosystems. Oikos 25:121-133.
- Stelmock, J.J. and Dean, F.C. 1979. Vegetation trampling effects analysis- 1975 plots, Mount McKinley National Park, Alaska. Final Report for National Park Service Contract No.Cx-9000-8-0154.
- Svensson, J. 1984. Effekten på Calluna vulgaris av kaniners bete. Dep. of Plant Ecology, Univ. of Lund (mimeografed).
- Warming, E. 1908. The structure and biology of arctic flowering plants. I. Ericineae. Medd. om Grönland 36.
- Vegetationskartor över svenska fjällkedjan. 1979-84. Liber Kartor, Stockholm.

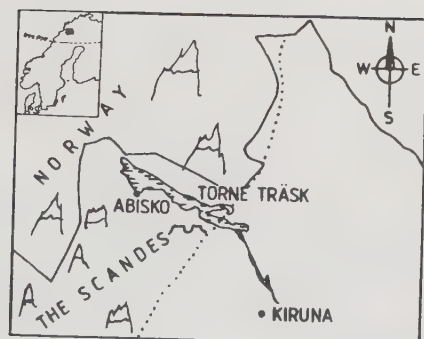


Fig.1a

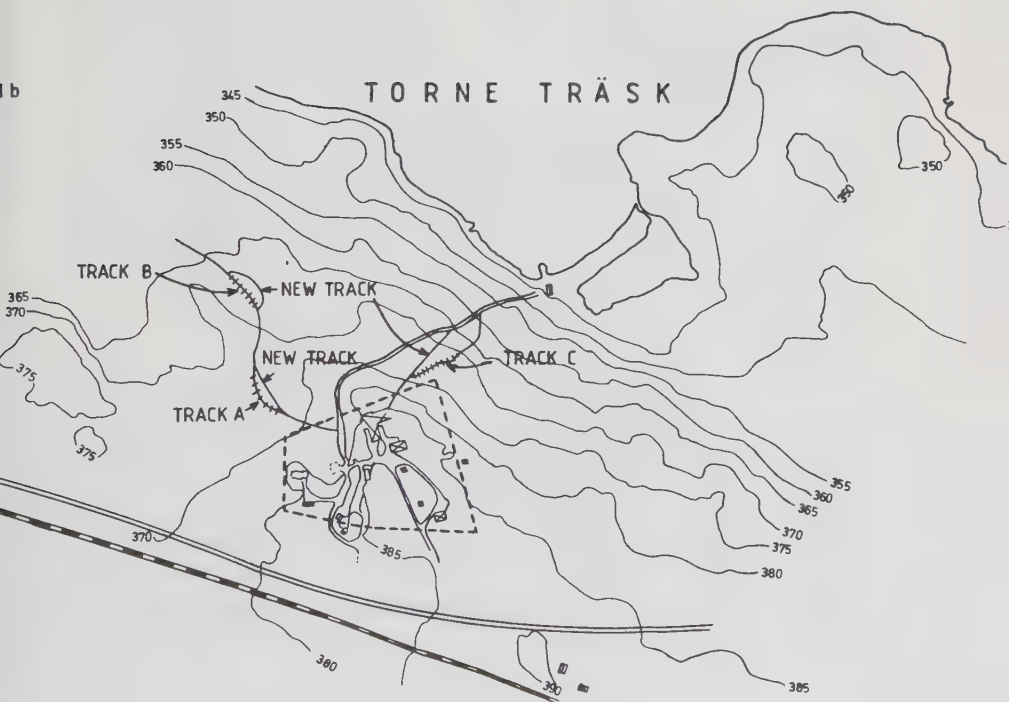


Fig. 1 Map of northern Lapland in Sweden showing Abisko on the southern shore of Lake Torneträsk (a), and detailed map of the area of Abisko Scientific Research Station and the locations of the three tracks studied in this paper (b).

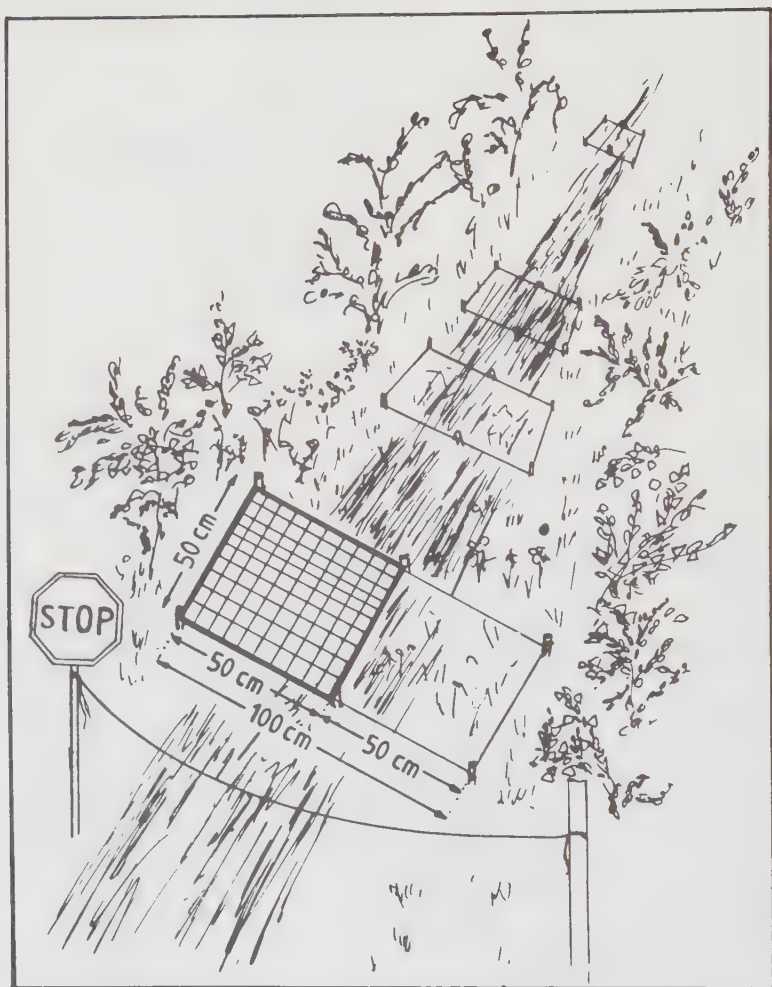


Fig. 2 Design of trampling experiments: Four transects, randomly established on the track, each containing 200 sample squares measuring 5 x 5 cm.

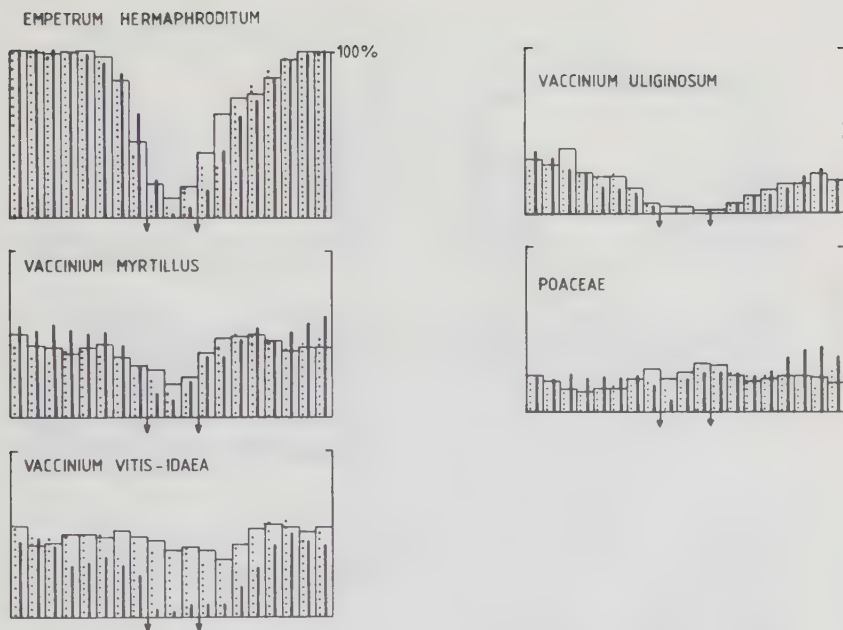


Fig. 3 Location and mean frequencies of a number of species in the four randomly selected transects across track A. Only species occurring in all four investigated transects are shown. Data are presented for a three-year period. Black bar=1978, Dotted bar=1979, Open bar=1980. Arrows denote the part of the track on which 90% of the trampling occurs according to a pilot investigation (see text 2.1). Deschampsia flexuosa represents 95% of the grasses (Poaceae).

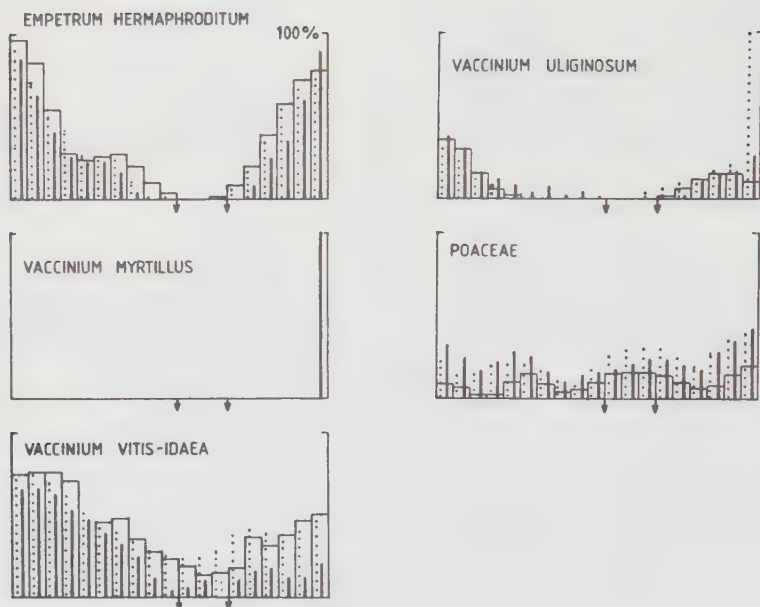


Fig. 4 Data for track B as described in Fig. 3 above. Vaccinium myrtillus is absent here and the grasses (Poaceae) are: Festuca ovina, 70%; Deschampsia flexuosa, 10%; Calamagrostis lapponica, 10%; other grasses and sedges, 10%.

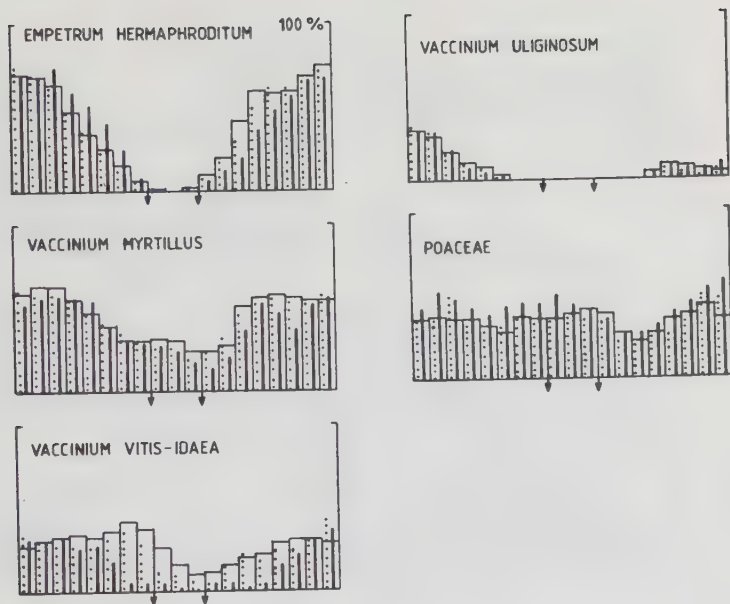


Fig. 5 Data for track C as described in Fig. 3 above. The grasses (Poaceae) consisted of Deschampsia flexuosa (80%) and Calamagrostis lapponica (20%).

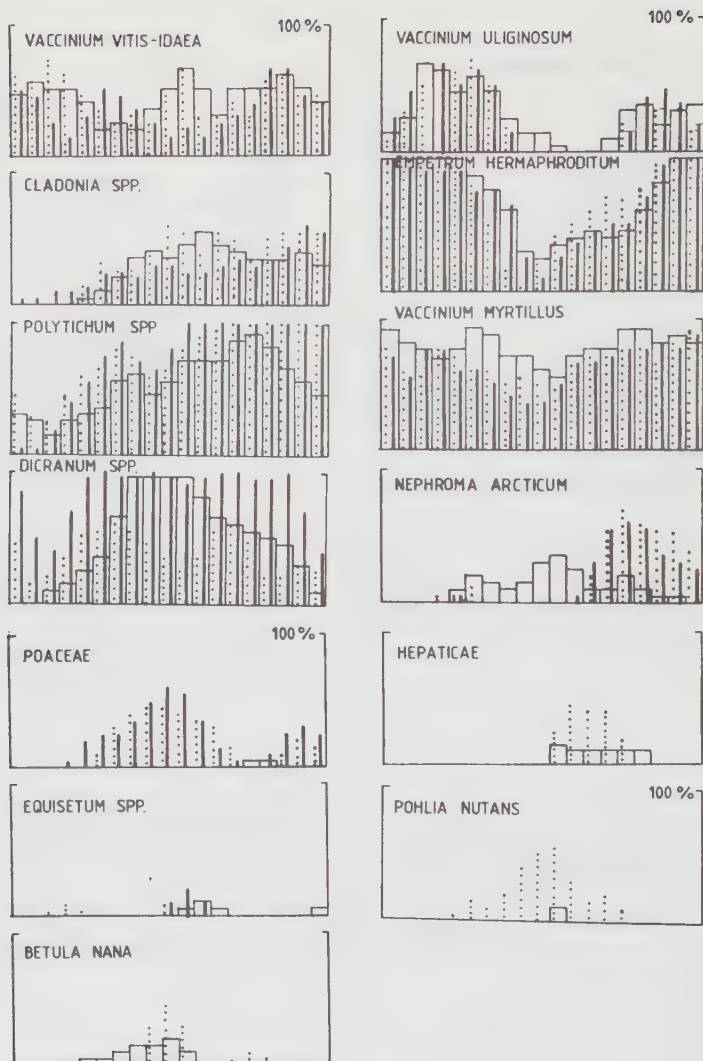


Fig. 6 An example of data from a single transect on track A.

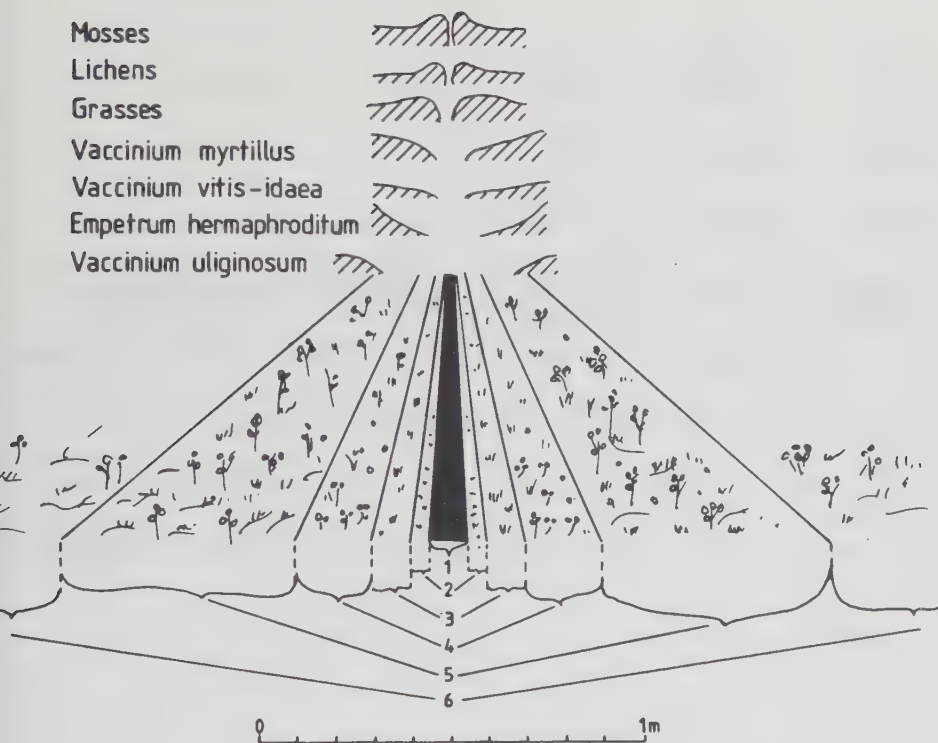


Fig. 7 Principle zonation of vegetation along a track passing through mesic to dry *Empetrum* heath, assuming that the track has been trampled for the past 5 years and that there has been intense trampling for one month at the beginning of the growing season. This figure is based on data from all of the 12 transects studied here and should be compared with the detailed description of a single transect presented in Fig. 6. Relative frequensis of some of the major life forms and species indicated in the upper figures.

1=Earth zone. 2=Earth-cryptogam zone. 3=Grass-cryptogam zone.
 4=Grass-*Vaccinium* zone. 5=*Empetrum*-*Vaccinium* zone.
 6=Virgin zone.

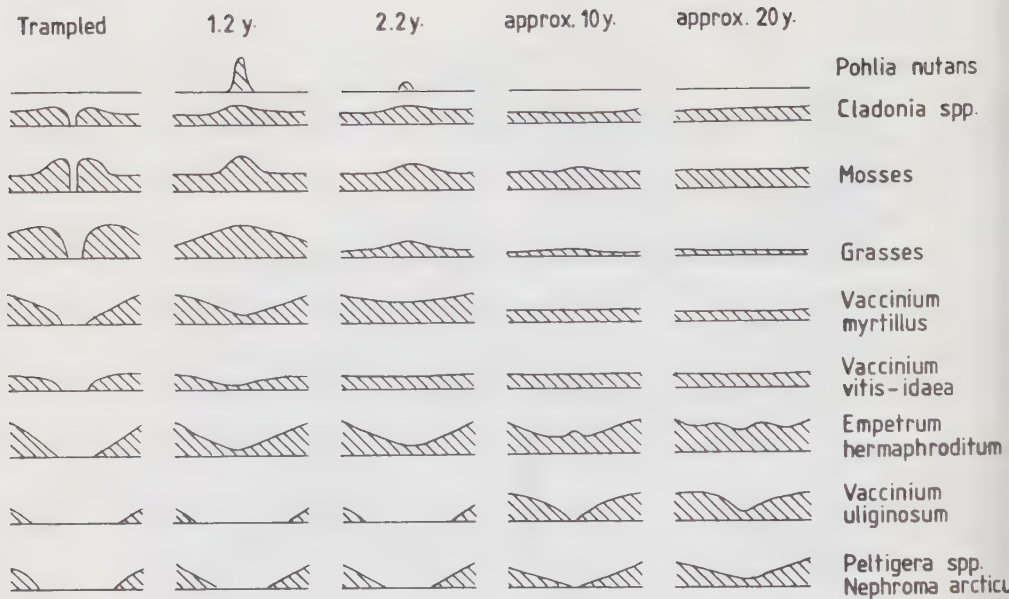


Fig. 8 The revegetation of tracks passing through *Empetrum* vegetation. The first column represent a currently trampled track whereas the second and third columns represent tracks disused for 1.2 and 2.2 years, respectively (based upon data collected from tracks A, B and C). Columns 4 and 5 are based upon data collected from 3 and 4 transects, respectively, from many different tracks in the Torneträsk area. Cf. Table 2. The height of the hatched areas denotes frequency of species across the track.

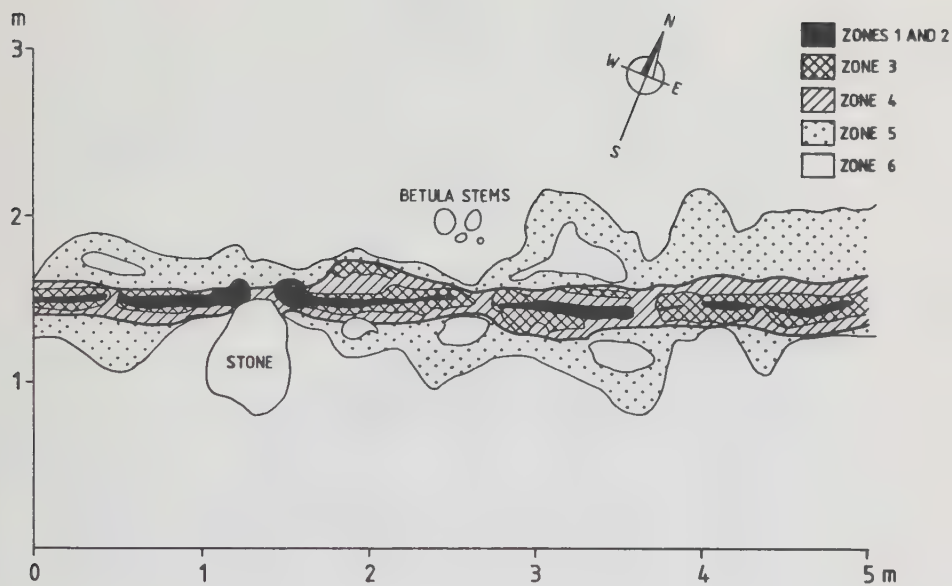


Fig. 9 Plan of a part of track A with the 6 zones as described in Fig. 7.

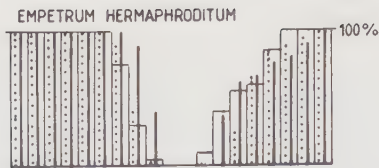


Fig. 10 The development of Empetrum hermaphroditum during the revegetation of track A, transect 2. For symbols see Fig. 3. This species often advances for one year, but then dies and retreats before advancing a second time.

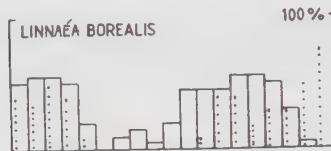


Fig. 11 The development of Linnaea borealis in the revegetation of track C, transect 2. For symbols see Fig. 3. This species is an example of a fast colonizer. Note the lack of black bars.



Fig. 12 The development of Diapensia lapponica on track B, transect 2. For symbols see Fig. 3.

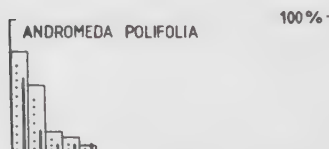


Fig. 13 The development of Andromeda polifolia on track C, transect 2. For symbols see Fig. 3. This species is an example of a poor colonizer.

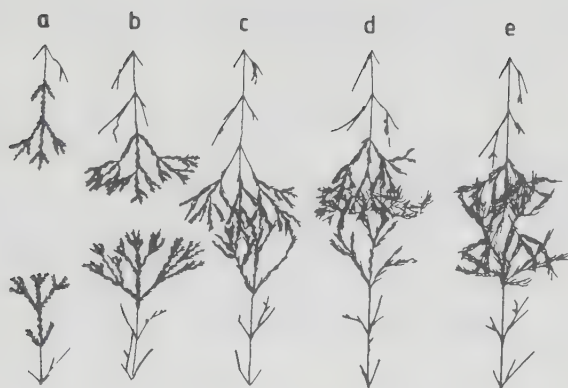


Fig. 14 *Empetrum hermaphroditum* colonizes disused tracks in the Torneträsk area almost entirely by the growth of vegetative shoots above ground. Only shoots aged 3 years or younger will have green leaves. As *Empetrum* advances (a-c), a green fringe is formed behind which is found a zone of older shoots without green leaves. After the two green zones have met (c,d), they advance to the sides of the track where they remain as two zones (e). This process is more marked in vegetation of dry, rather than wet habitats. Drawing based on photographs from track A.

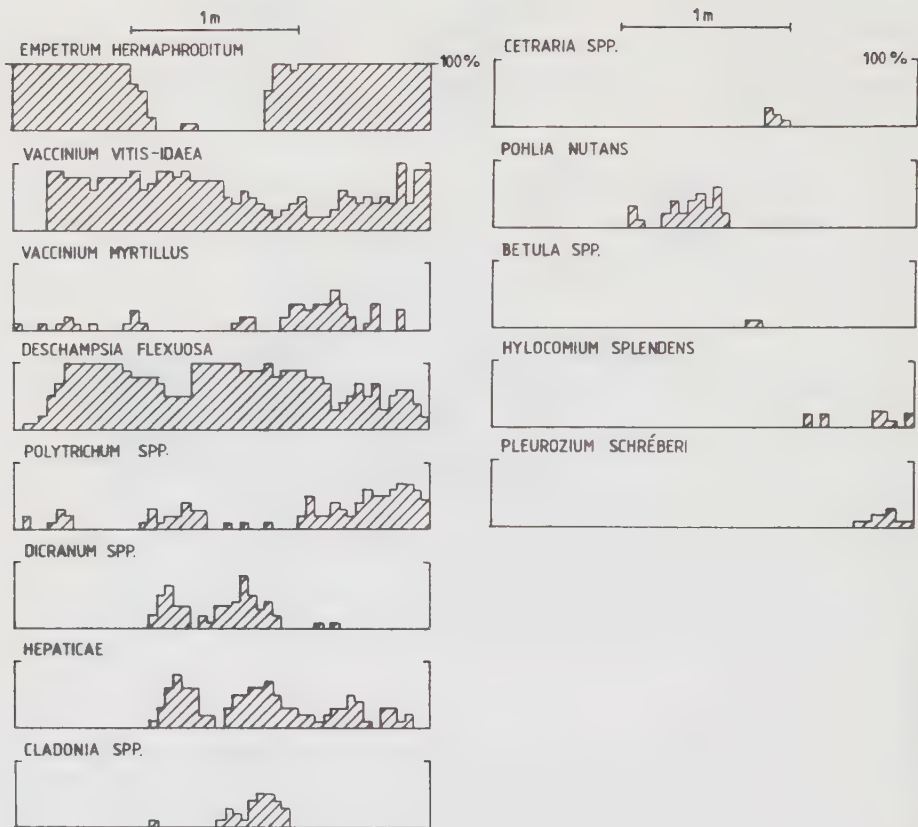


Fig. 15 Transect across a track which has not been trampled for the previous 12 years but which formerly was probably trampled by 3000 to 5000 people each year. The track is broader than the experimental tracks A, B and C and its bordering vegetation is very similar to that surrounding track B. The vegetation on the track has not recovered as well as that on narrower tracks with similar past histories (compare with Table 2). The height of the hatched areas denotes frequency of species across the track.

Table 1

Differences in frequency between the years 1978, 1979 and 1980 of a range of species from tracks A, B and C shown in Fig. 1. Four randomly located transects (columns:c1-c4) were established on each of the tracks. The left part of each column presents the frequency differences between the years 1978 and 1979, whereas the right part presents data for the years 1979 and 1980. + denotes an increase in frequency over all, or part of the transect whereas - denotes a corresponding decrease in frequency. (+) denotes an increase in frequency over 60% or more of the transect and decreases may have occurred over the remaining 40%. Similarly, (-) denotes a decrease in frequency over 60% or more of the transect. 0 denotes no marked change in frequency over the whole transect. This means that decreases or increase in growth may not be more than 60% in order to be placed in this category. Lack of symbols denotes incomplete data or absence of the species.

	A				B				C			
	c1	c2	c3	c4	c1	c2	c3	c4	c1	c2	c3	c4
<i>Empetrum hermaphroditum</i>	++	++	++	++	++	-0	+(-)	++	+0	++		00
<i>Vaccinium myrtillus</i>	+0	0+	++	++					-0	+0	++	+0
<i>Vaccinium vitis-idaea</i>	++	+0	+0	+0	+0	+0	++	+0	++	+0	+0	+-
<i>Vaccinium uliginosum</i>	00	+0	+0	-0+	00	(+)	0	0(-)			-0	--
<i>Betula nana</i>	++	++	++		+-	-+	00	0+	0+	+0		+0
<i>Betula pubescens</i>						+-	+-	+-				
<i>Arctostaphylos alpina</i>					00		00	00				
<i>Loiseleuria procumbens</i>					+(+)	00	00	+(+)				
<i>Linnaea borealis</i>									+-	++	++	
<i>Diapensia lapponica</i>					++							
<i>Andromeda polifolia</i>					++	+0	00					
<i>Salix phylicifolia</i>					00							
<i>Pinguicula vulgaris</i>					+-							
<i>Calamagrostis lapponica</i>	++	0+	--									
<i>Deschampsia flexuosa</i>					--	--	(+)(-)	--				
<i>Festuca ovina</i>									0+	-(-)	--	--
DICRANACEAE		-+	0+		--		+-					+0
POLYTRICHACEAE	--	-+	-+		++	-0	++	0-	00	0+	-+	
HEPATICAE	--	-0	0-		--	--	+-	(-)-	00	+-	+-	-
<i>Pohlia nutans</i>	+(+)	+(+)	+(+)		+(+)		+(+)	+(+)	+(+)	+(+)	++	++
<i>Pleurozium schreberi</i>	+(0)	+(+)	+-		--							+0
<i>Cladonia</i> spp.	+0	++	++		+-	+(0)	+-	+-	++	++	+-	+-
<i>Nephroma arcticum</i>	+0	00	00						0-	++	00	
<i>Cetraria</i> spp.	++			+-								

Table 2

Percentage cover of some vascular plants and cryptogams in a 30 cm wide zone in the middle of some old tracks in northwest Torne lappmark. Data were recorded during the years 1978 to 1981. The number of years since the track was last used is presented in the table and the cover of vegetation bordering the tracks is shown in brackets.

All the tracks were passing through dwarf shrub vegetation, but the wetness of the sites varied; VD=very dry, D=dry, M=mesic, W=wet.

Location of the track	number of years the track has been abandoned	soil type	veg. type	% cover cryptog.	% cover phanerog.
Abisko	12	sandy till	D	90(95)	50(90)
Abisko	4	clayey till	M	90	70
Delta of Alesättn	20	sandy till	D	80	50
Delta of Alesättn	20	sand	VD	70	50
Ladjojaure	5	sand	M	70	60
Laksjön (Abisko)	8	stony till	D	70	60
Nakerjaure	11	clay	W	90	90
Jieprenjåkk	25	silty till	M	90(95)	80(95)
Kärkevagge	40	peat	M	100(100)	80(90)
Alajaure	60	peat	W	90(95)	70(90)
Stordalen	6	peat	W	70(90)	60(80)

